TREE STORIES ABOUT A PEATLAND:

TREE-RING RECONSTRUCTIONS OF WATER TABLE AND LARCH SAWFLY OUTBREAKS IN SASKATCHEWAN

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By

MAGALI FURLAN NEHEMY

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ABSTRACT

Eastern larch (*Larix laricina*) and black spruce (*Picea mariana*) are the most dominant tree species in peatlands in Canada, however interactions between peatland hydrology and species-specific radial growth are poorly understood. This study investigates the relationships between the growth/hydrological response of eastern larch and black spruce across a topographical gradient within a peatland in Saskatchewan. Tree-ring analysis revealed that peatland hydrology is the main factor driving radial-tree growth. Black spruce on the edge of the fen showed a positive relationship to increased water-table level, while eastern larch in the fen revealed a negative correlation to water-table level rise. Further analysis illustrated that radial-tree growth response to hydrology is dependent on specific water-table levels according to species and micro-site. Identified thresholds indicated that only 8 cm of variability in water-table level can greatly affect the fen forest dynamics. Once the relationship between tree ring and hydrology was established, a multiple- species regression equation was derived from tree-ring data to reconstruct past water-table levels. Results indicated that eastern larch and black spruce are suitable proxies to reconstruct hydrological variability at the site.

Eastern larch ring widths are not only subjected to change by hydrology, but they can also be altered by exposure to larch sawfly outbreaks (*Pristiphora erichsonii*). Researchers have often been limited in their ability to draw accurate conclusions regarding the history of sawfly outbreaks in peatlands. Water-table level suppressions result in similar radial-growth patterns as when trees are defoliated by larch sawfly, making accurate diagnoses of larch sawfly outbreak a challenge. In this study I investigated the relationship between sawfly outbreaks and peatland hydrology. Five outbreaks where identified using traditional dendroecological analysis. The last outbreak identified was found to be a result of hydrological growth suppression and not sawfly defoliation. Observations indicated that periods of low water-table level may lead to increased populations of larch sawfly in northern Saskatchewan. I stress the necessity of using long-term hydrological analyses to accurately infer outbreak periods to distinguish them from water-table suppression.

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DEDICATION

To vovô Zizinho (Abrahão Miguel Nehemy)

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AMS	Average mean sensitivity
BERMS	Boreal Ecosystem Research and Monitoring Sites
BSEF	Black spruce chronology from outer edge of the FEN
BSO	Black spruce chronology from OBS
EPS	Expressed population signal
FEN	Fen site from BERMS
LACF	Eastern larch chronology from centre of the FEN
LAEF	Eastern larch chronology from inner edge of the FEN
LAO	Eastern larch chronology from OBS
m asl	Metres above sea level
m	Metres
MSI	Mean inter-series correlation
OBS	Old Black Spruce Site from BERMS
RWI	Ring-width index
µm	Micrometres

CHAPTER 1: INTRODUCTION

1.1Introduction

Northern biomes are undergoing rapid climate change, and an increase in temperature is expected to impact hydrological processes within these sensitive environments (IPCC 2013). In these biomes, one of the most common landscapes features are peatlands, which are characterized as permanently water-saturated ecosystems with poorly drained organic soils (National Wetlands Working Group 1997; Rydin and Jeglum, 2013). About 90% of the Earth's peatlands are located in the northern hemisphere (Strack, 2008). Peatlands store about 10% of the global surface freshwater (Holden, 2005), and represent one third of total global soil carbon (approximately 600 Gt of carbon) (Yu, 2012).

The hydrology of peatlands plays a pivotal role in driving the ecological processes within an ecosystem (Rydin and Jeglum 2013). Water-table level controls plant community composition (Robroek *et al.*, 2007; Breeuwer *et al.*, 2009; Walker *et al.*, 2015), carbon allocations and flux (Gazovic *et al.*, 2010; Mitsch *et al.*, 2013), organic matter decomposition (Straková *et al.*, 2012) and nitrogen gas flux (Freeman, Lock and Reynolds, 1993; Regina *et al.*, 1996; Choi, Chang and Bhatti, 2007). Northern-latitude peatland wetness is expected to change under future climate change scenarios (Roulet *et al.*, 1992). Predicted climate-induced change in temperature and precipitation could result in water-table drawdown or inundation (Moore, 2002; Tarnocai, 2006, 2009; Pachauri and Reisinger, 2007). Reliable long-term records of water-table fluctuations are therefore needed to advance our knowledge of the temporal variability of hydrological process, to better understand its impact and interaction with other important processes in peatlands and advancing our knowledge about possible impacts of climate change that will occur in the future.

Dendrochronological studies have successfully used ring widths as a proxy for climate records (Gray, Graumlich and Betancourt, 2007; Stahle *et al.*, 2007; Birks *et al.*, 2014; Schofield *et al.*, 2016; Shi *et al.*, 2016), and are being investigated as a potential proxy for water-table fluctuations in European peatlands (Dauškane, Brūmelis and Elferts, 2011; Smiljanić *et al.*, 2014). Previous studies have indicated that trees inhabiting peatlands are usually small and slow-growing because of the hypoxic conditions in the roots zone promoted by water-table level,

indicating that water-table depth may be the most limiting factor to radial-tree growth in this environment (Lieffers and Rothwell, 1987; Linderholm, Moberg and Grudd, 2002; Pepin, Plamondon and Britel, 2002; Cedro and Lamentowicz, 2011; Dauškane, Brūmelis and Elferts, 2011; Edvardsson *et al.*, 2015).

Compared to other methods of peatland water-table reconstruction (*e.g.*, testate amoebae; Swindles *et al.*, 2015), tree-ring widths have greater and finer temporal resolution (Hughes, 2002; Smiljanić *et al.*, 2014). Climate sensitive species are good proxies for climate variability; their ring-width patterns vary distinctly year-to-year in accordance to a limiting parameter of the climate (Speer 2010). Eastern larch (*Larix laricina* (Du Roi) K. Koch) and black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb.) inhabit northern peatlands and are considered climate and flood sensitive (Islam and Macdonald, 2004; Girardin *et al.*, 2005; Mamet and Kershaw, 2011; Walker and Johnstone, 2014), which indicates that these species may have great potential as a proxy for water-table fluctuation in Canadian peatlands.

Trees growing in peatlands are not only subjected to climate and hydrology, but also exposed to natural disturbances such as fires and insect outbreaks (Brassard and Chen, 2006). An increase in insect outbreaks incidence and intensity in the boreal forest is expected with predicted increases in global warming (Volney and Fleming, 2000). Insect outbreaks lead to changes in forest landscape and affect its ability to provide ecosystem services (Brassard and Chen, 2006; Schowalter, 2012). In the Canadian boreal forest, insects are the major disturbance agents affecting forest productivity and increasing tree mortality (Candau and Fleming, 2011). In 2014, 20.3 million hectares (ha) of forest were damaged by insects (representing 7% of the total forest in the country), while fire only affected 4.6 million ha (Natural Resources Canada, 2015, 2016). Larch sawfly (*Pristiphora erichsonii* Htg.) is a major defoliator of eastern larch in North America (Coppel and Leius 1955; Ives 1976). The history of larch sawfly in the Canadian boreal forest is well explored in eastern Canadian provinces, however few studies have reported its occurrence and intensity in Saskatchewan (Nairn *et al.*, 1962; Case and Macdonald, 2003a).

Dendroecology has been a useful tool to date larch sawfly outbreaks (Jardon, Filion and Conrad, 1994; Bergeron *et al.*, 2002; Case and Macdonald, 2003a; Girardin *et al.*, 2005; Nishimura and Laroque, 2010). Larch sawfly defoliation periods cause significant decrease in radial-tree growth, which is indicated by the presence of narrow and locally absent rings (Jardon, Filion and Conrad, 1994; Bergeron *et al.*, 2002). However, a critical issue not yet addressed in

the literature exists when distinguishing larch sawfly outbreaks from adverse changes in hydric regimes. The rise of water-table level in peatlands can also induce changes in tree-ring widths and an increase incidence of locally absent rings (Linderholm, Moberg and Grudd, 2002; Cedro and Lamentowicz, 2011; Smiljanić *et al.*, 2014; Edvardsson *et al.*, 2015), which may lead to a misinterpretation of outbreak history or reconstruction of water-table variability in peatland environments. Previous outbreak studies have already pointed out that "indistinguishable" periods of growth suppression caused by flooding and larch sawfly defoliation would produce similar results in the ring pattern (Nairn *et al.*, 1962; Ives and Nairn 1966; Girardin *et al.*, 2005). Therefore, a need to advance an understanding in the relationship between larch sawfly outbreaks and flooding regimes exists, to accurately deconstruct outbreak periods and water-table level changes in peatlands using tree rings.

1.2 Research objectives and thesis outline

The purpose of this thesis is to investigate the potential use of eastern larch and black spruce as a proxy for peatland water-table variability in Canada. To do this, I utilized established dendrochronological techniques to explore the link between radial-tree growth, water-table level, climate, and insect outbreaks in a case study in northern Saskatchewan. I developed and performed my research at long-term research sites, the BERMS (Boreal Ecosystem Research and Monitoring Sites), specifically at the FEN (an open moderate-rich minerotrophic fen) and OBS (Old Black Spruce Site), located within the Boreal Plain Ecozone.

This thesis is organized in five chapters with two stand-alone but related manuscripts. The first manuscript (Chapter 3 – *"A multi-species dendrohydrological reconstruction of water-table variability from a peatland in northern Saskatchewan"*) investigates the impact of spatial and temporal variability of water-table level in the radial growth of trees inhabiting peatlands in Canada. In this manuscript, dendrohydrological methods were applied to better understand the relationship between black spruce and eastern larch radial growth with water-table levels and climate. Past hydrological variability of the site was also reconstructed through the use of ring widths.The following research questions were examined:

1. Does water-table level affect eastern larch and black spruce radial growth in the fen?

2. Are there water-table level thresholds that dictate changes in tree species composition in the fen?
3. Can the annual water-table record of the fen be extended back in time with the use of larch and black spruce as a proxy tree-ring source?

In the second manuscript (Chapter 4 - *Understanding the influence of peatland hydrology on larch sawfly (Pristiphora erichsonii (Hartig) outbreak*) the relationship between water-table variability and larch sawfly outbreaks in peatlands was investigated. In this manuscript, a novel approach was used to reconstruct larch sawfly outbreak history by combining established dendroecological techniques and peatland hydrological data, to distinguish between growth suppressions. The specific research question is:

4. Are larch sawfly outbreaks related to water-table variability in peatlands?

CHAPTER 2: LITERATURE REVIEW

This literature review will explore the links between radial-tree growth, water-table level and larch sawfly occurrence in peatland ecosystems from a dendrochronological perspective. First, it described the global importance of peatlands, their susceptibility to climate change, and the role of the water table in driving ecological processes while focusing on peatland hydrology and tree-growth dynamics. Second, it described the use and importance of proxies to understand past climate variability. Third, it discussed the potential use of dendrochronology by exploring dendroclimatology as a tool for paleoclimate reconstructions, and the advances in dendrohydrology, and the need to investigate the potential use of tree ring to reconstruct hydroclimatic events in peatlands. Next, it described two common North American peatland tree species and their potential relationship with water-table level, thus justifying the use of the species ring widths as a suitable proxy for water-table level in peatlands. Following this, the literature review identified potential adverse effects on radial-tree growth in Canadian peatlands by introducing the field of dendroecology, and described the impact of larch sawfly in peatland trees, and the importance of understanding mixed sources of variables affecting radial-tree growth. Lastly, it identified the main gaps in the literature regarding peatland dendrohydrology, and the novelty of this research.

2.1. Peatlands

2.1.1 Peatland ecosystems

Peatlands are defined as water-saturated ecosystems with poorly drained peat soils (National Wetlands Working Group 1997; Rydin and Jeglum, 2013). Peat is the partially decomposed remains of plant tissues accumulated under low oxygen environments (Rydin and Jeglum, 2013). Representing only 3% of the Earth´s landscape area (Gorham, 1991; Dahl and Zoltai, 1997), peatlands play an important role in sequestering large amounts of atmospheric carbon (Gorham, 1991; Dahl and Zoltai, 1997; Hilbert, Roulet and Moore, 2000). Aside from

holding one third of the global soil carbon pool (about 600 Gt of global C) (Yu *et al.*, 2010), peatlands store 10% of the global surface freshwater (Moore, 2002; Holden, 2005).

About 90% of peatlands are found in the northern hemisphere (International Peat Society, 2008). In Canada, this ecosystem has the largest concentration in the Boreal Wetland Region (64%), followed by the Subarctic Wetland Region (33%) (Tarnocai, 2006). Canada represents about 25% of peatland's total earth surface (Dahl and Zoltai, 1997), of which 70% are forested (Moore, 2002). In continental western Canada (Alberta, Saskatchewan and Manitoba), peatlands cover an area of approximately 36.5Mha (Lemprière *et al.*, 2013).

There are four different ecosystem classes for peatlands – marsh, swamp, fen and bog (National Wetlands Working Group 1997; Rydin and Jeglum, 2013), with the most dominant classes in Canada being fens and bogs (Tarnocai, 2009) (Figure 1.1). Bogs represent 67% of the total peatland area and fens cover 32%, while the 1% remaining is represented by marshes and swamps (Tarnocai, 2006). Bogs are ombrotrophic peatlands, with limited connection to groundwater sources (Mitsch and Gosselink 2000; Rydin and Jeglum 2013). Nutrient and water inputs are mainly from atmospheric deposition (Glaser *et al.*, 1981; Gunnarsson, Rydin and Sjörs, 2000). Fens are minerotrophic peatlands with groundwater supplies comprised of high concentrations of minerals compared to bogs (Rydin and Jeglum 2013). The hydrological and chemical differences between fens and bogs affect the surface floristic compositions (Edvardsson *et al.*, 2016). Fens are usually inhabited by vascular plants (*e.g.*, sedges) and brown mosses (Amblystegiaceae family), while bogs are typically dominated by peatmosses (Sphagnaceae family) and other small vascular plants (Edvardsson *et al.*, 2016). Both peatland types are also inhabited by tree species. In Canada, the most common tree species found in peatlands are black spruce and eastern larch.

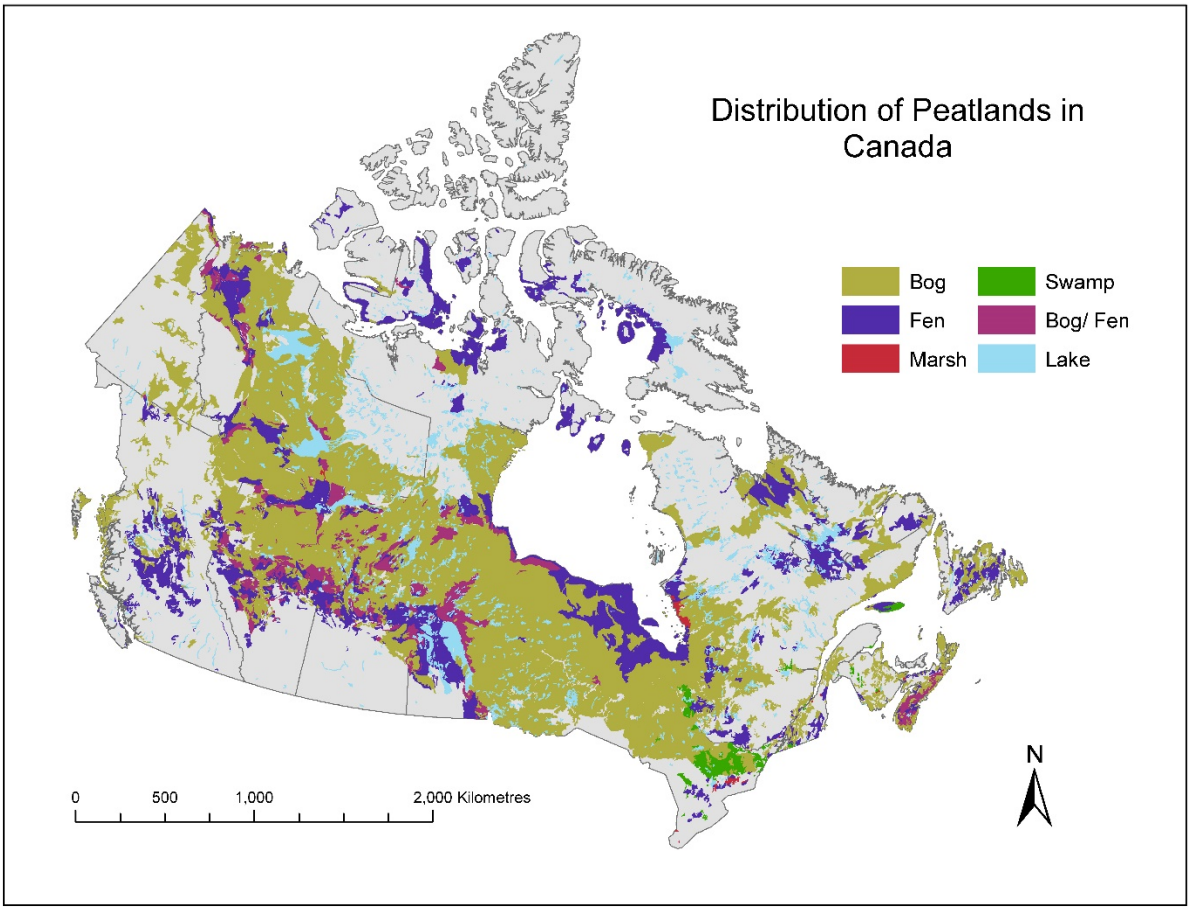

Figure 2. 1 Map of the peatlands distribution in Canada. Projected coordinate system: Lambert Conformal Conic, NAD83. Source: Tarnocai et al., 2011 (peatland data); ESRI Canada, Natural Earth Vector (Canada base map).

2.1.2 Climate change and consequences to northern peatlands

Boreal, Subarctic and Southern Arctic regions are expected to experience the greatest effects of climate change, where the majority (59%) of peatland ecosystems in Canada are situated (Tarnocai, 2006). An increase in atmospheric temperature and alterations to precipitation patterns are forecasted for the 21st century (IPCC 2013; Mekis and Vincent 2011; Vincent et al. 2012). Future warming is likely to alter the structure and function of many ecosystems, as well as their ability to provide services (Shafer, Bartlein, and Thompson 2001; Fischlin et al. 2007; Fischlin et al. 2009; Price et al. 2013). Canadian Global Climate Models predict an increase in average-annual temperature of 3-4°C by 2020 and 5-10°C by 2050 in Canada (Hengeveld 2000).

During historical times, a significant increase in seasonal rainfall has been observed across Canada, while snowfall increased mainly in the north, but a substantial decline in annual

snowfall has been observed in the southwestern part of the country between 1950 and 2009 (Mekis and Vincent, 2011). As a result of the close relationship between climate and the hydrological cycle, water availability will be significantly affected both spatially and temporally due to climate change in the future (Creutzfeldt, Heinrich and Merz, 2015).

Predicted changes in water availability are likely to alter water-table levels (Roulet *et al.*, 1992; Hilbert, Roulet and Moore, 2000), because fluctuations in peatlands are a function of soil-water storage determined by the balances between precipitation, evapotranspiration, and the discharge and recharge of groundwater (Gunnarsson, Granberg and Nilsson, 2004; Gong *et al.*, 2012). In a drier scenario, the water-table level of peatlands is expected to drawdown as a consequence of an increase in air temperature, evapotranspiration rates and drought periods (Pachauri and Reisinger, 2007; Wang, Hogg and Price, 2014). In a wetter scenario, water-table levels could rise as a consequence of an increase in seasonal precipitation (Moore, 2002). A decrease in water-table level would lead to a process of shifting peatlands from a net carbon sink to a net carbon source (Hilbert, Roulet and Moore, 2000; Trettin *et al.*, 2006), resulting in a decline of peat accumulation (Waddington *et al.*, 2010) which would ultimately modify peatland vegetation communities composition (Breeuwer *et al.*, 2009; Chivers *et al.*, 2009; Munir *et al.*, 2014).

Water table ranks high among the key factors controlling important ecological process in peatlands (Rydin and Jeglum 2013; Gong et al. 2012). Water-table level affects not only the soil carbon balance (Trettin *et al.*, 2006), but also plant community composition (Laine, Vasander and Laiho, 1995; Minkkinen *et al.*, 1999; Zona *et al.*, 2009; Munir *et al.*, 2014), photosynthetic efficiency of plants (Kettunen, 2002), respiration (Mäkiranta *et al.*, 2009) and net ecosystem production (Hilbert, Roulet and Moore, 2000). Therefore, understanding water-table variability over long-time scales is important to help to predict future climatic impacts in peatland processes and their ability to provide ecosystem services.

2.1.3 Peatland water-table dynamic and trees

High water-table levels in peatlands affect tree growth due the adverse environmental conditions that they create. In water-logged soils, trees are subject to low oxygen (hypoxic conditions) within the rooting zone. This affects a wide range of physiological processes including gas exchange, reduction in transpiration rates and stomatal conductance, reduced

photosynthetic rates, reduced carbohydrate metabolism and reduced hydraulic conductivity (Pepin, Plamondon and Britel, 2002; Islam, MacDonald and Zwiazek, 2003; Herschbach *et al.*, 2005; Herrera *et al.*, 2008). Therefore, not all plant species are adapted or can survive in peatland environments. In a peatland rewetting event, after 60 years of drainage and agricultural activities, oak (*Quercus robur* L.) trees could not adapt to the new water-table level, and many of them growing in low lying areas died due to the water-logging conditions (Scharnweber *et al.*, 2015). Other studies have also pointed out that similar changes in peatland hydrology can greatly affect ecosystem dynamics and lead to changes in species composition (Laine, Vasander and Laiho, 1995; Minkkinen *et al.*, 1999; Laiho *et al.*, 2003; Breeuwer *et al.*, 2009; Potvin *et al.*, 2015).

Even with the lack of long-term hydrological data (Razavi *et al.*, 2015; Elshorbagy *et al.*, 2016) tree-ring studies in peatlands have already pointed out that peatland hydrology is the main factor controlling radial-tree growth, suggesting that climatological factors, such as temperature and precipitation may only play secondary roles in these environments (Boggie, 1972; Cedro and Lamentowicz, 2011; Dauškane, Brūmelis and Elferts, 2011; Smiljanić *et al.*, 2014; Edvardsson *et al.*, 2015). However, direct comparison of tree-ring data with hydrological records to fully comprehend fine scale tree-growth variability is lacking. Therefore, any study that present long-term hydrological records and has access to living-tree data may be an asset to better understand tree response to hydrological variability in peatlands.

The evidence of water-table level as a main factor controlling tree development is also evident in observations of increasing tree growth and changes in stand structure following peatland drainage (Dang and Lieffers, 1989a; Macdonald and Yin, 1999; Frelechoux *et al.*, 2000). The new environment promoted by drainage illustrates improvement in edaphic conditions, such as increases in temperature and nutrient availability, and improved aeration (Lieffers and Rothwell, 1986b; Macdonald and Lieffers, 1990; Macdonald and Yin, 1999; Prévost, Plamondon and Belleau, 1999; Choi, Chang and Bhatti, 2007). The evidence of peatland hydrology as the limiting factor to plant species development is also evident through observations of increases in peatland respiration and primary productivity after the net lowering of the regional water-table level (Sulman *et al.*, 2009). However, positive relationships are not the only potential condition to be found with a decrease in water-table levels in peatlands. Tree species inhabiting peatland habitats have also illustrated moisture stress in periods of low water-table levels (Pepin, Plamondon and Britel, 2002). Therefore, the investigation of tree-radial

growth and natural hydrological variability in peatlands over long-time scales is necessary to improve our understanding of peatland development in the environment. Understanding the impact of fine-scale changes of peatland hydrology on tree growth can help to identify potential tipping points in ecosystem shifts in response to changing climates (Scheffer et al. 2012).

2.1.4 Impact of trees on peatland ecosystem and hydrology

Peatland hydrology can affect tree species composition and growth, but trees can also affect hydrological process in this ecosystems. The effects of changes in tree and shrub densities on peatland functioning and services are complex (Limpens *et al.*, 2014). In treed peatlands, trees can potentially affect the rate of peatland carbon storage if photosynthetic and carbon fixation capacity are reduced to lower rates than that of decomposition (Linderholm and Leine, 2004; Juutinen, Bubier and Moore, 2010). Besides affecting peatland carbon cycling, the presence or increase in tree cover is likely to affect the peatland environment by potentially increasing soil nutrient availability by inputting nutrients through litter fall, decreasing solar radiation by providing shade, decreasing air temperature, and consequently reducing decomposition rates by promoting a cooler environment (Ohlson *et al.*, 2001; Eppinga *et al.*, 2009; Straková *et al.*, 2012). Trees can also decrease the influence of wind, by reducing wind speed (Kellner, 2001). All of the environmental changes mentioned above could provide a more suitable environment for the development of vascular plants (Ohlson *et al.*, 2001; Holmgren *et al.*, 2015), potentially increasing their establishment and triggering positive feedbacks that can promote a shift towards a more treed and denser environment (Scheffer et al. 2001; Scheffer et al. 2012). Changes in tree density presents an important impact in peatland hydrology by increasing transpiration and precipitation canopy interception (Limpens *et al.*, 2014).

However, a non-linear relationship between tree density and peatland water loss has also been observed (Limpens *et al.*, 2014). In a controlled environment, peatlands with higher tree density had higher water-table levels, followed by peatlands without trees, and the lower water-table level was related to low tree density (Limpens *et al.*, 2014). It is believed that fewer trees can promote peat drying and increase transpiration rates, conversely, with the increase in canopy density, the microclimate of the environment is altered by reducing evapotranspiration rates (Heijmans, Arp and Chapin, 2004). Therefore, in striving to understand these complex

interaction between peatland hydrology and tree growth, it is fundamental to better understand the future impact of climate change on peatland forest ecosystems and water cycling.

2.2 Proxy records

Long-term instrumental records are scarce around the world (Bradley 2011; Elshorbagy *et al*., 2016). Western European instrumental records are the longest records in the world, and they only extend back to the late seventeenth century (Bradley 2011). This situation restricts many researchers to relatively short period of observations to understand long-term environmental variability (Bradley 2011). The long-term perspective is extremely important for studies that are trying to understand long-term processes, extreme climatic conditions and rare events, such as non-stationary in climatic and hydrological processes, severe droughts, and volcanic eruptions (Bradley 2001; Razavi *et al*., 2015). Due to the lack of long-term data, it is unlikely that researchers fully comprehend the entire spectrum of climate variability and processes of important events (Bradley 2011; Razavi *et al.*, 2015). In order to address this problem, it is necessary to invest in high-resolution proxy resources.

High-resolution natural proxies present exclusive opportunities to better comprehend climate variability through time because they lengthen the limited observation interval that is provided from short-term instrumental records (Bradley 2011; Razavi *et al.*, 2015). However, in order to achieve high resolution and acquire reliable paleoclimatical data, it is necessary to meet some requirements such as: replicability of the archive sampled to reduce uncertainties and avoid misinterpretations due to missing data (*e.g*., layers (ice cores), rings (trees)); the archive contains seasonal to annual resolution; the relationship between the proxy being studied and the environment is, to a moderate degree, understood; the principle of uniformitarianism is respected by the proxy investigated (this will be explained in section 2.3 Dendrochronology); and, the archive is sensitive to climate variability over a wide range of time (Bradley 2011).

Tree rings, among many other natural archives (*e.g.*, ice cores, corals, varved sediments), have shown to be a superior proxy to hydrological and climatological records (Crawford, Griffin and Kipfmueller, 2015; Razavi *et al.*, 2015; Elshorbagy *et al.*, 2016) and many climatological reconstructions have been successfully developed in both hemispheres using tree-ring records (McCarroll and Loader, 2004; Meko, 2006; St. George *et al.*, 2009; Brienen *et al.*, 2013; Birks *et al.*, 2014; Stoffel *et al.*, 2015; Edvardsson *et al.*, 2016). The common use of tree rings as a proxy

to extend hydrological and climatological records has been due to their ability to easily achieve the above-listed requirements, as seen as essential for effective proxies.

Trees are widely dispersed in different environments and are easily accessible, while recording important information present in the environments they inhabit. Also, achieving high replicability of the archive is relatively easy and inexpensive, requiring only the use of an increment borer to increase the number of samples collected. Another advantage of the use of tree rings is the relative low cost of the analysis when compared to other proxies. Most importantly, tree rings provide the highest accuracy and precision at fine temporal scales, providing annual to sub-annual resolution (Speer 2010; Hughes 2011; Luckman 2013). When using tree-rings proxies it is the possible to use more than one variable at the same time, such as the opportunity of combining the use of ring width and isotopes (McCarroll and Loader, 2004).

2.3 Dendrochronology

Dendrochronology is the science that studies tree rings, dating and interpreting information such as ring width, density or isotope composition, recorded in the wood structure (Fritts 1976; Speer 2010). Dendrochronological data are broadly used to reconstruct past events, describing temporal and spatial distribution of geomorphic, atmospheric or ecological episodes in the environment, such as insect outbreak (Nishimura and Laroque, 2010), fire (Sibold and Veblen, 2006), floods (Therrell and Bialecki, 2014), meteoroid events (e.g., Tuguska event in Siberia) (Vaganov *et al.*, 1999) and even earthquakes (Van Arsdale *et al.*, 1998).

The annual variability of tree-ring records can be accurately determined using crossdating techniques, providing potential proxies for environmental factors that affect tree growth in the year that the environmental factor was altered (Luckman, 2013). This process is based on the fact that trees of the same species, growing in the same location, experience similar environmental conditions, and therefore present similar resultant growth patterns (Fritts 1976; Speer 2010). Crossdating is the process of pattern matching tree-ring widths, to determine the ring boundaries between series, in order to evaluate data quality and to secure a tree-ring pattern representing a group (Speer 2010). For crossdating to be effective, the ring parameters need to vary synchronously, reproducing a common response to an external variable (Luckman, 2013).

Tree-rings are good proxies only for those variables that strongly limit tree growth (Frits 1976; Speer 2010; Luckman, 2013), this is commonly known as the “principle of limiting

factors" (Speer 2010). The principle of limiting factor states that the most environmental limiting factor will control radial-tree growth (Fritts, 1976; Speer, 2010). A limiting factor is the main variable recorded in the ring width, resulting in a series of rings that fluctuate in width in response to that variable (Speer, 2010). In treed peatlands, for example, water-table level strongly limits trees development (Boggie, 1972; Linderholm, Moberg and Grudd, 2002; Smiljanić *et al.*, 2014). A high water-table level decreases the availability of oxygen to tree roots, while a low water-table level can cause drought stress (Dang and Lieffers, 1989a; Pepin, Plamondon and Britel, 2002). Based on this information, year-to-year ring-width variability can often be correlated to the limiting variable (Fritts, 1976; Speer, 2010). This principle is based on Liegbig´s law of the minimum (Speer, 2010).

Another principle that dendrochronological studies are founded upon is the principle of uniformitarianism. The principle of uniformitarianism states that "the present is the key to the past", which means that the environmental variables that control tree-radial growth are constant through time (Fritts, 1976; Speer, 2010). Besides the principle of limiting factor and uniformitarianism, another important principle in dendrochronology is the principle of site selection. This principle highlights the importance of maximizing the signal recorded in trees. In order to achieve a clear signal from the variable of interest, sites should be located where the trees are the most likely to be stressed by that variable (Speer, 2010).

Even high-resolution records might have low-frequency components that diverge from the range of the climatic environment in which they are inserted (Speer, 2010; Hughes, 2011). The appearance of low-frequency signals in chronologies are in many cases a consequence of tree biological growth, and so they therefore must be first removed before the extraction of the environmental signal of interest can be used (Speer, 2010; Hughes, 2011). The low-frequency signals are defined by the signal-to-noise ratio, the amount of wanted information recorded in the tree-ring record, versus the amount of undesired information and random variability recorded within the chronology (Speer, 2010). Standardization processes are often applied to chronologies in order to extract the desired signal, and eliminate the unwanted noise (Speer, 2010). By fitting curves to trends in tree-ring series, age-related and site-related growth rates can be removed. However, the standardization technique must be related to the nature of the study. For example, an ecologist that is studying dynamics in forest stands over a short period of time may be

interested in short-term variability in the chronology, whereas a climatologist would often be more interested in the long-term climate variability recorded within the same ring patterns.

2.3.1 Dendrohydrology

Proxy-climate reconstructions are important to better understand current and future climate changes (Charman *et al.*, 2012). Dendroclimatological studies have been successfully used to document frequency and geographical distribution of past drought episodes and high precipitation periods (Hughes, Swetnam and Diaz, 2011), through seasonal temperature and precipitation reconstructions (*e.g*., Gray *et al*. 2007, Stahle *et al*. 2007). However, investigating water-table level changes using tree rings has not been the focus of much research (Charman *et al.*, 2012).

Dendrohydrology (a subfield of dendroclimatology) is the science that studies tree-ring properties of moisture-sensitive trees to explore and reconstruct past hydrologic variables, such as floods and stream flow (Denneler, Bergeron and Bégin, 2010; Lara *et al.*, 2014; Therrell and Bialecki, 2014; DeRose *et al.*, 2015; Saito *et al.*, 2015). Achieving an accurate understanding of hydroclimatic variability is challenging, since most proxy-climate records are sensitive to temperature, and limited chronologies present hydroclimatological signs (Charman *et al.*, 2012). Dendrohydrological studies have revealed that tree-ring measurements from stands of long-lived moisture-sensitive trees are a reliable source of proxy-hydroclimatic data, and provide accurate long-term chronologies with high resolution (Sauchyn *et al.*, 2015). However, the use of tree rings to study water-table variability is limited to a few cases in the world (Linderholm, Moberg and Grudd, 2002; Nossov, Ruess and Hollingsworth, 2010; Bogino and Jobbágy, 2011; Dauškane, Brūmelis and Elferts, 2011).

2.3.2 Dendrohydrology in practice: peatland environments

The potential use of tree-ring width as a proxy for water-table level has been explored in northern peatlands (Linderholm, Moberg and Grudd, 2002; Dauškane, Brūmelis and Elferts, 2011; Smiljanić *et al.*, 2014), however only one species was investigated. In a Sweden peatland, Scots pine (*Pinus sylvestris* L.) was used to investigate the relationship between the species and water-table level, but they found radial growth was mainly influenced by the growth season air temperature and precipitation (Linderholm, Moberg and Grudd, 2002). *P. sylvestris* responded to water-table variability indirectly, by changes in evapotranspiration rates (Linderholm, Moberg

and Grudd, 2002). In another study conducted in Latvian bogs, a Scots pine chronology illustrated a direct correlation to growing season air temperature and precipitation (Dauškane, Brūmelis and Elferts, 2011). The authors discussed that the lack of correlation to water-table level may be a result of the absence of an available long series of water-table measurements.

A dendrochronological investigation of Scots pine growing in a peatland in Estonia indicated that the water-table level was the main factor influencing growth, and therefore, tree-ring width is a potential proxy for water-table reconstruction in the right situation (Smiljanić *et al.*, 2014). According to the authors, long-term water-table records are necessary to cross-calibrate and detect structural changes in the tree-growth records. A dendroclimatological study conducted in a Finnish bog explored the relationship between *P. sylvestris* tree-ring widths and climate, and found that trees growing on the edge of the bog presented different chronologies from trees growing in the center of the bog (Cedro and Lamentowicz, 2011). According to the authors, the chronologies from trees at the edge presented a strong correlation to temperature, while they could not identify the main limiting factor on tree growth from trees within the center of the bog. They speculated that trees in the center of the bog may have been responding to the changes from the water-table level, however it was not tested due to the lack of hydrological data available in their study (Cedro and Lamentowicz, 2011). Yet, despite the importance of peatlands and their hydrological variability to global-carbon storage questions, there is no evidence of a suitable tree species to reconstruct water-table level in peatlands in Canada.

2.3.3 Sensitive tree species

Climate sensitivity is defined as the magnitude to which a system is affected by climate-related stimuli (IPCC, 2001). The sensitivity of a species depends on a variety of factors such as ecophysiology and microhabitat preferences (Dawson et al. 2011). In dendrochronology, a tree-ring chronology is considered sensitive when ring-width patterns vary distinctly from year-to-year (Speer, 2010). Generally, it illustrates that the species is responding to an overriding stimuli, common to the entire group of trees, such as climate. Trees are able to record this information within their rings, and therefore, the chronology is considered climate-sensitive. Conversely, species that are not climate sensitive usually present a complacent ring-width series with relative small to no annual variability existing (Speer 2010). Therefore, to achieve reliable results using tree rings as a proxy, it is important that the tree is sensitive to the limiting variable.

A common statistic calculated for measuring how sensitive a series is to this year-to-year variability is mean sensitivity (MS) (Grissino-Mayer 2001; Speer 2010). The MS value ranges from 0.0 on the complacent side to 1.0 on the sensitive side. Series that have MS values around 0.0 illustrate low variability within ring-width values, whereas, series with great variability in ring-width have higher values. Values between 0.10 and 0.19 are considered low mean sensitivity values, while values between 0.20 and 0.29 are considered intermediate, and MS values above 0.30 represent high-sensitivity series (Grissino-Mayer 2001).

2.4 Eastern larch and black spruce

The *Larix* genus is composed of ten species distributed throughout the cooler parts of the Northern Hemisphere. Only three of the ten species are native to Canada, while the others inhabit European and Asian forests (Farrar 1995). *Larix occidentalis* (Nutt.), *Larix lyallii* (Parl.) and *Larix laricina* ((Du Roi) K. Koch) are the only three species native to Canada. The species *Larix laricina*, known as eastern larch or tamarack, presents the widest distribution across North America. It is a deciduous coniferous species occurring in the boreal forest and found in all provinces of Canada (Cheliak, Wang and Pitel, 1988; Sims, Kershaw and Wickware, 1990). Eastern larch is classified as a pioneer to early successional species, usually colonizing open peatlands in association with black spruce (Sims, Kershaw and Wickware, 1990). It can also be found in drier habitats growing in association with white spruce (Brook, 2001; Monson, 2003; Girardin *et al.*, 2005).

The *Picea* genus is composed of 40 species distributed through the cooler portions of the Northern Temperate Zone (Farrar 1995). There are seven species that are native of North America, and five species are found in Canada, including black spruce (*Picea mariana* [Mill] BSP) (Farrar, 1995). Black spruce is an evergreen coniferous species that grows in pure or mixed stands (Sims, Kershaw and Wickware, 1990). Black spruce can be found in mixed stands growing in association with white spruce (*Picea glauca* [Moench] Voss), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx), balsam fir (*Abies balsamea* (L.) Miller), and or white birch (*Betula papyrifera* Marsh) on upland soils (Johnston 1990). In peat plateaus, it is often found growing in association with eastern larch trees (Johnston 1990). Black spruce is considered a pioneer to mid-successional species (Sims, Kershaw and Wickware, 1990).

Eastern larch is a deciduous conifer and shade intolerant species, shedding its entire canopy during the fall (Tilton, 1977; Sims, Kershaw and Wickware, 1990). Being a coniferous deciduous species, eastern larch translocates high amounts of nutrients present in the leaf back into the tree, before shedding needles in the fall of each year (Gower and Richards, 1990; Killinbeck, 1996). Black spruce is an evergreen coniferous and a shade-tolerant species, the species invests resources to produce wax cuticles to its long-lived multi-year leaves, allowing for superior water and nutrient retention (Sims, Kershaw and Wickware, 1990; Islam and Macdonald, 2005).

Eastern larch and black spruce tolerate a wide range of temperatures, from moderate to cold regimes, and under a wide variation of precipitation regimes, from dry subarctic Alaskan sites with a mean-annual precipitation of 170 mm, to eastern Canadian wetlands with a mean annual precipitation of 1400 mm (Sims, Kershaw and Wickware, 1990). Both species are also highly tolerant of frost events, commonly occurring in early-fall and late-spring within peatland ecosystems (Krajina et al. 1982). Black spruce grows in a variety of soil conditions and within a variety of hydrological regimes, it is found in dry shallow upland mineral soil, to wet lowland organic soils (Sims, Kershaw and Wickware, 1990). Eastern larch also grows in a wide range of soils, from shallow coarse-textured to deep organic soils (Sims, Kershaw and Wickware, 1990). Ideal conditions for eastern larch growth is on well-drained loamy soils close to water bodies, however it is relatively rare to find the species in this environment because eastern larch is easily outcompeted by other trees (Johnston 1990; Sims, Kershaw, and Wickware 1990). Both species present a high tolerance to flood, however eastern larch is more tolerant to prolonged flooding as it has advantages in its morphological traits to better resist the impacts of flooding, relative to black spruce (Sims, Kershaw and Wickware, 1990; Montague and Givnish, 1996; Islam and Macdonald, 2004).

The root system of both species growing in peatlands is shallow (maximum depth of 30 cm) and wide (about 3 m), predominantly inhabiting the unsaturated substrate above the water table (Strong and La Roi, 1983a; Lieffers and Rothwell, 1987). Comparing both species, eastern larch trees are usually represented with higher amounts of fine roots, about 14% of its biomass, while black spruce is only 4%, and both species present low development of vertical roots (Strong and La Roi, 1983a). In mineral soil, the presence of a taproot is rare, and absent in

organic soil (Fowells, 1965), however black spruce is more prone to developed a tap root when compared to eastern larch (Strong and La Roi, 1983a).

In peatland habitats, both species exhibit a wide tolerance to their environment, growing from oligrotrophic nutrient-poor bogs, to minerotrophic nutrient-rich fens (Tilton, 1977; Montague and Givnish, 1996). In peatlands, eastern larch tends to dominate the higher moisture sites, usually spots associated with water flow, while black spruce tends to dominate drier portions of the landscape, usually ombrotrophic peat domes, slightly raised ridges that receive little ground water input (Tilton, 1977; Kenkel, 1987; Montague and Givnish, 1996; Evans *et al.*, 2016). Despite some understanding of the different performance of both species in peatland environments and the knowledge of the ecophysiological advantage of eastern larch over black spruce regarding the ability to sustain better growth rates under hypoxic conditions (Islam and Macdonald, 2004; Calvo-Polanco, Señorans and Zwiazek, 2012), little is known about the radial-growth response of both species to fine scale hydrological variability in peatlands.

2.4.1 Climate relationship

Previous studies have illustrated that eastern larch and black spruce are sensitive to changes in climatic conditions, mainly related to moisture availability, and so are able to provide qualitative records of past environmental variability (Bonkoungou, Raynal and Geis, 1983; Girardin, Tardif and Bergeron, 2001; Girardin *et al.*, 2005; Huang *et al.*, 2009; Walker and Johnstone, 2014). Eastern larch is more climatically sensitive as a species than either black or white spruce growing in the same environment (Mamet and Kershaw, 2011), and is also more tolerant to flooding than black spruce in minerotrophic soils (Islam, MacDonald and Zwiazek, 2003; Islam and Macdonald, 2004). In Prince Albert National Park (Saskatchewan, Canada), a tree-ring study indicated that eastern larch growing in peatland environments was sensitive to moisture availability and evaporative stress (Case and Macdonald, 2003). Narrow rings were observed when winter precipitation was low, and consequently provided low water input in the bogs through snow melt in the spring (Case and Macdonald, 2003). A study conducted in central Saskatchewan, indicated that black spruce are very sensitive to precipitation when compared to jack pine (*Pinus banksiana* Lamb.) (Bouriaud, Frank and Bhatti, 2014). The authors suggested this great difference in sensitivity is related to the difference in roots system between both species, as jack pine develops a tap root system being able to access deeper ground water than black spruce that presents a shallow root system and is more dependent on precipitation to raise

the water-table level at the site. Other studies illustrated that during drier periods, black spruce decreased their stomatal conductance in a quick response to the drying of the top layer of the peat (Pepin, Plamondon and Britel, 2002), which then decreases their radial growth. A diverse range of studies have already reported negative correlations between temperature and black spruce radial growth (Huang *et al.*, 2009; Drobyshev *et al.*, 2013; Walker and Johnstone, 2014).

In studies conducted in post-drainage peatlands sites, eastern larch respond better to the drainage stimuli than black spruce, resulting in greater radial growth (Lieffers and Rothwell, 1987; Macdonald and Lieffers, 1990; Macdonald and Yin, 1999). Being a coniferous-deciduous species with indeterminate radial growth of long shoots, while black spruce is an evergreen species with determinate growth of short shoots, eastern larch is able to adapt more quickly to changes in environmental conditions (Clausen and Kozlowski, 1967; Macdonald and Yin, 1999). Eastern larch also has an intrinsically faster growth rate and a root system with more fine-root biomass, which gives it a greater ability to take up nitrogen than black spruce (Strong and La Roi 1983; Lieffers and Rothwell 1987; Macdonald and Lieffers 1990).

2.5 Dendroecology

In their natural environment, trees are not only affected by climatological and hydrological factors, they are also subjected to ecological disturbances, such as fire and insect defoliation (Volney and Fleming, 2000; Brassard and Chen, 2006; Candau and Fleming, 2011). Tree rings can also provide valuable high-resolution information of the spatial/temporal distribution of ecological disturbances (Frits and Swetnam 1989). The field that investigates ecological processes and disturbances in forest ecosystems through tree rings is called dendroecology (Speer, 2010). One major field in dendroecology is the study of insect outbreaks. Tree rings can provide valuable evidence of insect outbreak history, allowing for a better understanding of insect population dynamics, including outbreak magnitude and distribution (Swetnan *et al.*, 1985; Speer *et al.*, 2010). Enhancing the knowledge of insect outbreaks are crucial to better understanding ecological dynamics and their interaction with climate (Pickett and White 1985). In addition, the knowledge about insect cycles is critical for better forest management practices because they can provide understanding of an insect's impact on forest productivity and provide better guidelines to model future risk and distribution of outbreaks.

2.5.1 Larch sawfly and water-table level

The occurrence of insect outbreaks are often associated with other disturbance agents, such as fire, or with climate regimes (Pohl, Hadley and Arabas, 2006). The recognition of historical ecological interactions can lead to a better understanding of insect outbreaks, equipping land managers with critical knowledge on future incidences of outbreaks and on how climate change may affect these disturbances. In North America, larch sawfly is a major defoliator of eastern larch (Coppel and Leius 1955; Ives, 1976). The causes or circumstances that lead to the occurrence of an outbreak, and the relationship between larch sawfly outbreaks and climate, is still not well understood. Investigations of insect cycles have provided evidence of climate influencing population survival rates. Lejeune (1955) revealed that high water-table level induces high mortality rates to larch sawfly populations. According to the author, the insect is susceptible to flooding during late summer when the larvae drop to the ground and begin spinning cocoons, and during the pupae phase when the cocoons are still on the ground in early spring. Previous studies have found that larch sawfly outbreaks in drier sites have higher intensity and duration when compared to more hydric sites (Tailleux and Cloutier, 1993; Girardin *et al.*, 2005). The authors have suggested that this is probably related to larch sawfly survival in flooded conditions imposed by the environment. Despite the knowledge about the impact of water-table level on larch sawfly survival, and some understanding about the intensity of outbreaks related to a site's hydric regime, there are still no explicit investigations about the relationship between water-table level variability and larch sawfly outbreak occurrences.

The improvement in qualitative and quantitative methodologies in outbreak analyses have enabled more confident results when dating larch sawfly periods. The use of a host/non-host species analysis uses species growing at the same site to identify larch sawfly outbreaks (Fritts and Swetnam 1989; Holmes and Swetnam, 1996). The development of the program OUTBREAK enabled the assessment of outbreak signatures mathematically through the comparison of host and non-host tree-ring chronologies (Swetnam *et al.*, 1995; Speer *et al.*, 2001). The indication of pale rings (light latewood rings) followed by growth depressions and missing rings has also proven to be a valuable tool when identifying periods of larch sawfly defoliation events (Jardon, Filion and Conrad, 1994; Liang, Filion and Cournoyer, 1997). However, even with more developed analysis, studies have still found it challenging to distinguish between outbreak periods from other climatological signals. Girardin et al. (2005),

for example, reported it difficult to identify whether a suppression was related to insect defoliation or years of high water-table level. A better understanding of the relationship between outbreak periods and site hydrological variability is needed to guide future larch sawfly outbreak research. Previous studies have already pointed out to the need of understanding local adverse effects on tree-radial growth that may misperceive the herbivore signal, impeding advances on the understanding of outbreak events (Trotter *et al.*, 2002).

2.6 Research gap

Dendrohydrological studies are used to study hydroclimatic patterns in the long term and predicting anticipated change in the future. The bulk of dendrohydrological studies have been focused on reconstructions of stream flow (*e.g.*, Beriault and Sauchyn 2006, Woodhouse and Lukas 2006, Axelson *et al.*, 2009, Lara *et al.*, 2014).Few studies have been dedicated to the reconstruction of groundwater levels (*e.g.*, Bogino and Jobbágy 2011, Perez-Valdivia and Sauchyn 2011) and fewer still are devoted to understanding water-table fluctuations in peatlands (*e.g.*, Dauškane et al. 2011, Smiljanić et al. 2014). The potential use of tree-ring width as a proxy for predicting water-table level in peatlands, especially in Canada, has not been well studied, creating a significant gap in research.

Eastern larch and black spruce can be found in various types of peatlands all across Canada and have been shown to be sensitive to climate and moisture variability (Girardin, Tardif and Bergeron, 2001; Girardin *et al.*, 2005; Mamet and Kershaw, 2011; Walker and Johnstone, 2014). This represents a large potential to create long-term water-table records from proxy data for northern peatland environments. The physiological and morphological characteristics of eastern larch and black spruce also make it a suitable candidate for dendrochronological studies in peatland ecosystems. Past studies have already provided evidence that both species have a great potential to explore the relationship between radial-tree growth and climate (Mamet and Kershaw, 2011; Dufour-Tremblay, Lévesque and Boudreau, 2012), and radial-tree growth and moisture variability (Nairn *et al.*, 1962; Girardin, Tardif and Bergeron, 2001; Islam, MacDonald and Zwiazek, 2003). But as of yet, the effects of water-table fluctuation on the development of eastern larch and black spruce are not clearly understood, especially with a fine-scale perspective.

In Saskatchewan, the majority of eastern larch trees are growing in peatland environments where they are also susceptible to larch sawfly (Nairn *et al.*, 1962; Case and Macdonald, 2003a). Historical reconstruction of insect outbreaks are important records to evaluate forest susceptibilities and possible changes to forest structure and species composition. Dendrochronological studies that reconstruct the outbreak history of larch sawfly in Canada have been conducted in different provinces, however the majority of the research is in Eastern Canada (Arquillière *et al.*, 1990; Tailleux and Cloutier, 1993; Jardon, Filion and Conrad, 1994; Girardin, Tardif and Bergeron, 2001, 2002; Girardin *et al.*, 2005; Nishimura and Laroque, 2010). In Saskatchewan, previous knowledge on outbreak histories are still limited, with just a few studies having reconstructed larch sawfly outbreaks in the province (Lejeune and Hildahl, 1954; Nairn et al., 1962; Case and Macdonald, 2003) creating a significant gap in the literature.

Understanding ecological and climatological processes that drive the occurrence of outbreaks are extremely important. It is known that larch sawfly populations are susceptible to flood periods, however there is no evidence in the literature indicating whether low water-table level can enhance the occurrence of larch sawfly outbreaks. Another gap exists in the literature regarding the investigation of larch sawfly and peatland hydrology over long-time scales. To be able to develop reliable tree rings as a proxy for water-table levels in peatlands, it is essential to distinguish the source of growth suppression and understand the complex interactions in the environment between the multiple factors affecting radial-tree growth. Understanding the relationship between water-table and larch sawfly is crucial to reconstruct past outbreak periods and water-table levels in peatlands with higher certainty.

2.7 Study sites

The study was conducted in the Boreal Ecosystem Research Monitoring Sites (BERMS) situated in the Boreal Plain Ecozone in the central portion of the province of Saskatchewan, Canada (Figure 2.2) (Barr *et al.*, 2012). This study focused on two of the permanent sampling plots from the BERMS network: a mature black spruce stand (OBS) and a fen site (FEN).. The BERMS sites are exposed to a continental climate with a long and dry cold season, followed by a short growing season (Barr *et al.*, 2012). The average length of the growing season is about 150 days (Rowe 1972). The mean annual January and July air temperature are, -17.9 and 16.2° C,

respectively. The mean annual precipitation is 467 mm, of which 30 % falls as snow (Barr *et al.*, 2012).

The OBS site is situated 30 km northeast of Candle Lake, near White Swan Lake (53.98°N, 105.11°W) (Balland *et al.*, 2006; Barr *et al.*, 2012). The stand is dominated by black spruce and eastern larch (Kalyn and Van Rees, 2006; Barr *et al.*, 2012). The understory is composed of mostly Labrador tea (*Ledum groenlandieum*), with a groundcover of Sphagnum spp. in wetter areas and feather mosses (*Hylocomium splendens* and *Pleurozium schreberi*), and lichens (*Claudina* sp.) in drier areas (Balland *et al.*, 2006; Kalyn and Van Rees, 2006; Barr *et al.*, 2012). The waterlogged sandy soil is covered by a peat layer (20-cm) (Barr *et al.*, 2012). The water-table depths at OBS vary from 0 to 1 m below the ground surface (Barr *et al.*, 2012).

The FEN is a 30.4 km^2 treed peatland situated about 40 Km southeast of OBS and 38 km north of Smeaton adjacent to Highway 106 (53.801N, 104.621W). It is classified as a minerotrophic patterned fen surrounded by black spruce and jack pine (*Pinus banksiana* Lamb) forest (Zoltai, Siltanen and Johnson, 2000). The fen extends about 6 km north to south and is approximately 1 km wide east to west at its widest portion. The FEN is mostly flat (1:1000 slope), with a 2 m drop in the southern portion (Hogan, 2006). The site is dominated by bog birch (*Betula pumila*) and eastern larch (Sonnentag *et al.*, 2010). Buckbean (*Menyanthes trifoliate*) and several sedge species (*Carex* and *Eriophorum* spp.) compose the understory (Sonnentag *et al.*, 2010). A thick layer of peat (from 2 to 3 m in the central portion, and about 0.5 to 1m on the edges) covers the soil (Sonnentag *et al.*, 2010; Barr *et al.*, 2012). The water table is usually at or above the peat surface, except in intensely dry years (Barr *et al.*, 2012).

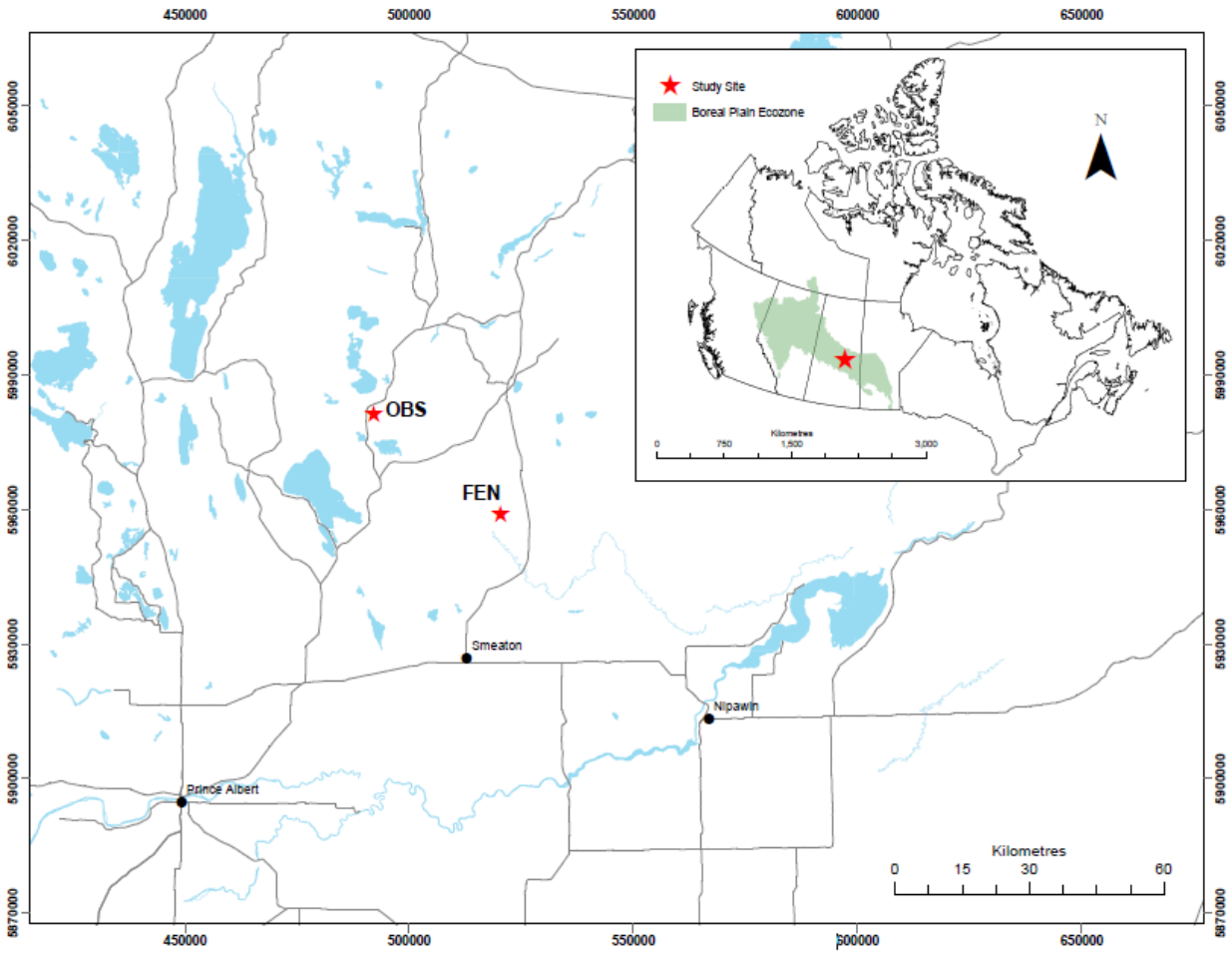

Figure 2. 2 Map of the locations of study sites (OBS and FEN) (red stars). Map of Canada (top right corner) and the Boreal Plains Ecozone (green) with locations of BERMS. Projected coordinate system: Lambert Conformal Conic. Source: ESRI Canada, Natural Earth Vector.

The study took place in the northern treed portion of the FEN, where water table records were also available. A clear forest gradient was observed in the site and three micro-environments were identified:

A) Outer edge: the canopy is composed by a dense black spruce forest. The ground is mostly covered by *Sphagnum* spp. moss and the peat depth varies from 0.1 to 0.5 m. This micro-site is also classified as transition zone between the jack pine forest and the peatland (peat depth below 0.4 m). This micro-environment is at a higher elevation compared to the following micro-environments (Figure 2.3 b.).

B) Inner edge: the canopy is more opened when compared to the outer edge, however it is dominated by eastern larch trees. The ground in the site is dominated by sedge species and shrubs. The black spruce trees present in the shallower portion of this

micro-environment are smaller in diameter when compared to the outer edge trees, and many are rotten or dead. The peat depth varies from 0.6 to 1.5 m (Figure 2.3 c.).

C) Centre: Site dominated by eastern larch, smaller in height and diameters when compared to the inner edge. The average height for the site is around 2, 5 m. The peat depth is greater than 1.5 m (Figure 2.3 d.).

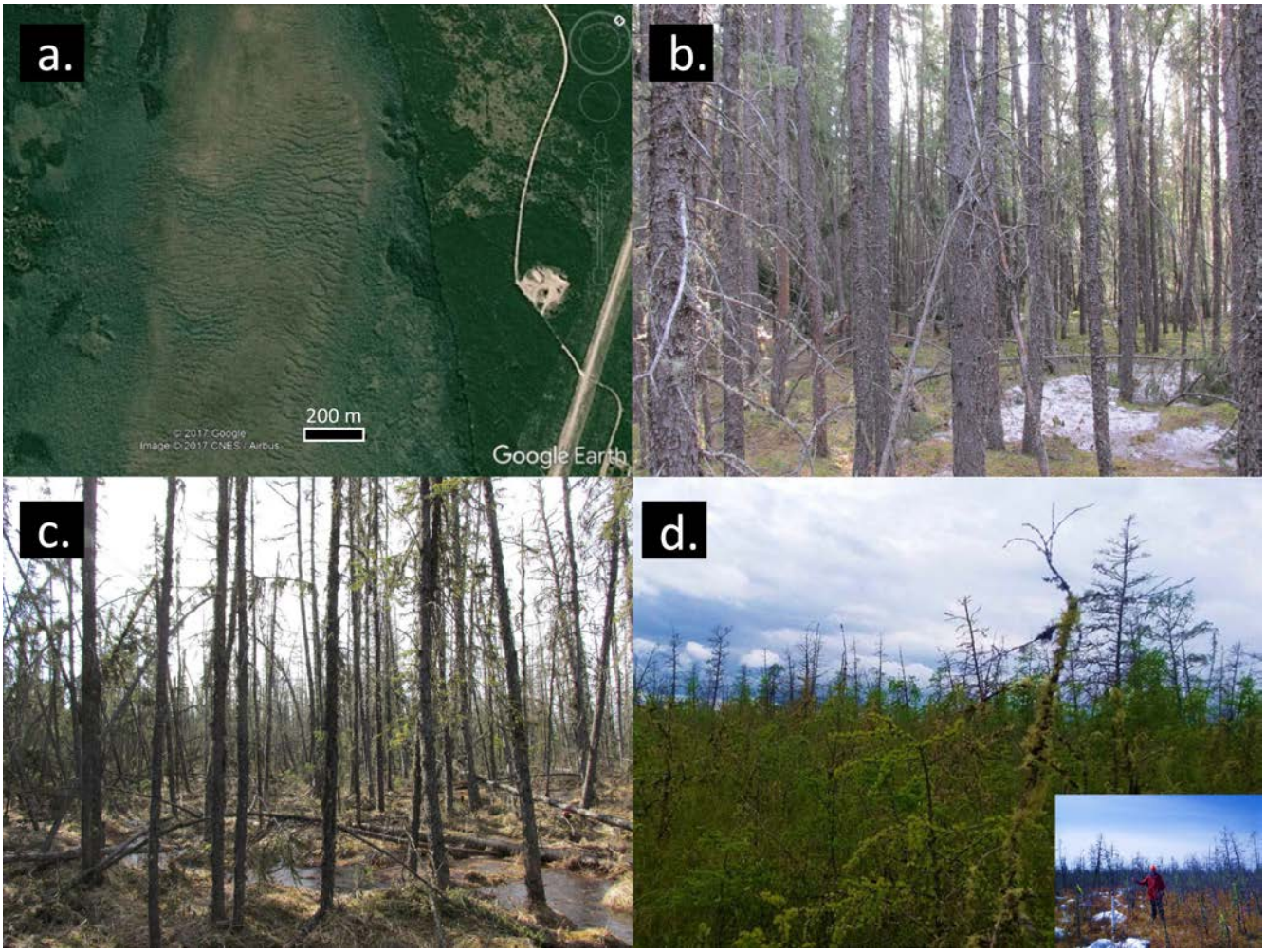

Figure 2. 3 FEN site. a. aerial image of the northern portion of the site (Google Earth, 2017); b. outer edge; c. inner edge; d. centre.

CHAPTER 3: A MULTI-SPECIES DENDROHYDROLOGICAL RECONSTRUCTION OF WATER-TABLE VARIABILITY FROM A PEATLAND IN SASKATCHEWAN

3.1 Abstract

This study explored the relationship between eastern larch and black spruce radial growth, the dominant tree species inhabiting peatlands in Canada, and peatland hydrology. This relationship was assessed across a gradient at the site. Dendrohydrological investigations of eastern larch and black spruce growing in a fen in central western Saskatchewan showed that water-table level is the main driver of cambial activity for both species in this environment. Climate (precipitation and temperature) do not illustrate any major influence on radial-tree growth variability in the fen. However, analyses indicated eastern larch and black spruce growing under the same hydrological regime, have an opposite relationship to water-table level. Black spruce responds positively to water-table rise, while eastern larch responded negatively to the same conditions. These differing responses were associated with species-specific physiological characteristics and micro-site conditions. The study further sought to understand how the relationship between tree species and peatland hydrology changes through time. Through a moving correlation analysis water-table threshold levels were pinpointed for each species at the site.

Results indicated that black spruce inhabiting the edge are negatively affected when water-table levels are below 487.68 m asl and responds positively when levels reach 487.73 m asl. Eastern larch inhabiting the inner edge of the fen indicate no response to water-table level when levels are below 487.72 m asl, however radial-tree growth is negatively affected when water table rose above this level. Eastern larch growing in the centre of the fen are affected by water-table levels that reach a threshold of 487.76 m asl, where they illustrate a consistent negative correlation to water-table levels in all time periods. Identified thresholds indicated that only 8 cm variability in the water table can greatly affect radial-tree growth in the studied site.

Once the relationship between radial tree growth and peatland hydrological was understood, a multiple species regression equation was derived from tree-ring data to reconstruct the water-table level at the site. The tree ring model explained 64% of the observational record. This research provides a better understanding of the sensitivity of a peatland forest to hydrological variability and sheds significant light on a more broad scale of the vulnerability of peatland forests in Canada.

3.2 Introduction

Peatlands cover only 3% of the earth´s surface (Dahl and Zoltai, 1997), but store about one third of the world soil carbon (473 – 621 Gt) (Dahl and Zoltai, 1997; Yu *et al.*, 2010). Canadian wetlands represent one quarter of the global wetlands, of which about 70% are forested (Dahl and Zoltai, 1997). Peatland´s high capacity for storing carbon is due to the water-logged conditions in the ecosystems avoiding peat exposure and decomposition, resulting in a consistent net excess of gross ecosystem productivity over respiration and decomposition rates (Moore, 2002). Greenhouse gas (CO_2 and CH_4) exchange between peatlands and the atmosphere likely have a direct impact on global climate systems (Frolking and Roulet, 2007). Despite the importance of peatlands to the global carbon cycle and sensitivity to hydrological dynamics, there is a lack of studies investigating long-term variability of peatland hydrology. A better understanding of peatland ecosystem's response to hydrological variability could potentially improve the certainty around land-atmosphere interface modelling, improve land management practices, and help the scientific community to anticipate responses to climate change in northern regions (Sulman *et al.*, 2009; Waddington *et al.*, 2014).

Peatland hydrological changes not only greatly affect global climate dynamics, they also drive plant species composition and abundance. Over long-time periods, hydrological changes can drive plant community succession altering ecosystem structure, which likely alters carbon cycling in peatlands (Bridgham *et al.*, 1995; Minkkinen and Laine, 1998; Strack and Waddington, 2007; White *et al.*, 2008; Talbot *et al.*, 2010; Potvin *et al.*, 2015). Peatland hydrology also affects the presence and density of trees, which, in turn, can potentially change peatland hydrology (Limpens *et al.*, 2014).

Ground-water flow and storage are frequently changing as a consequence of anthropogenic and climatic stressors (Alley *et al.*, 2002) and hydrological dynamics of peatlands at northern latitudes are expected to change under future climate-change scenarios (Roulet *et al.*,

1992; Bridgham *et al.*, 1995; Tarnocai, 2006; Trettin *et al.*, 2006). Models are predicting an increase in summer temperature and dryness (Wetherald and Manabe, 2002; Sheffield and Wood, 2008), but also an increase in summer precipitation (Wetherald and Manabe, 2002; Mekis and Vincent, 2011; Khaliq *et al.*, 2014; Masud, Khaliq and Wheater, 2016) leading to potentially significant impacts on hydrological cycles while also introducing uncertainties regarding future scenarios. Predicted climate-induced change in temperature and precipitation could result in water-table drawdown or inundation (Moore, 2002; Tarnocai, 2006, 2009; Pachauri and Reisinger, 2007). Reliable records of water-table fluctuations are therefore needed to advance our knowledge of the temporal variability of hydrological processes in peatlands, enhancing our understanding of ecosystem functioning and the impact of long-term changes in ecosystem dynamics.

However, observational records are usually scarce or too short to contain sufficient hydrological variability for understanding long-term processes (Elshorbagy *et al.*, 2016). The use of natural proxies is crucial to address this problem. Reconstruction of paleo-hydrology can be achieved through the use of different natural sources, such as tree rings, lake and stream sediments, ice layers, fossil pollen profiles, testate amoeba or fungal microfossils (*e.g.*, Baumgartner *et al.*, 1989; Loaiciga & Michaelsen 1993; Woodland *et al.*, 1998; Linsley *et al.*, 2004; Yeloff *et al.*, 2007; Leipe *et al.*, 2014). In particular, tree-rings can provide fine-scale temporal resolution data, which are widely available from different environments, and are relatively inexpensive to acquire (Hughes, Swetnam and Diaz, 2011; Luckman, 2013). In addition, tree-ring relationships can be directly tested against instrumental records, decreasing the uncertainty related with the interpretations of paleo-proxies (Charman *et al.*, 2004).

Tree rings have been used as proxies for hydrological variables such as groundwater levels (Ferguson and St. George 2003; Bogino and Jobbágy 2011; Perez-Valdivia and Sauchyn 2011), lake levels (Digerfeldt *et al.*, 1992; Meko 2006) and streamflow (Case and Macdonald 2003; Woodhouse and Lukas 2006; Axelson *et al.*, 2009; Hart *et al.*, 2010). However, the use of annual-tree growth to reconstruct past water-table variability in peatlands has not been well explored (Cedro and Lamentowicz, 2011; Smiljanić *et al.*, 2014), with a focus on investigating Scots pine (*Pinus sylvestris* L.) in European peatlands. Despite the potential use of eastern larch and black spruce in Canada (Lieffers and Rothwell, 1986a; Macdonald and Lieffers, 1990;

Rothwell, Silins and Hillman, 1996) to reconstruct hydrological records, no study has yet explored these species.

Tree growth in peatlands is mostly driven by water-table fluctuations (Boggie, 1972; Lieffers and Rothwell, 1987; Linderholm, Moberg and Grudd, 2002; Moir, Leroy and Helama, 2011; Edvardsson *et al.*, 2012, 2016; Smiljanić *et al.*, 2014). In order to survive in water-logged ecosystems, trees possess a shallow and wide-spreading root system (20 to 30 cm) distributed close to the surface, facilitating uptake of oxygen and nutrients (Strong and La Roi, 1983a; Lieffers and Rothwell, 1986a, 1987). High water-table levels can suppress radial growth due to root hypoxia and decreased nutrient availability in the cold, poorly aerated peat (Dang and Lieffers, 1989a; Islam, MacDonald and Zwiazek, 2003). Also, a significant net decrease of the water table to a level below the root zone may lead to water stress and consequent decrease in growth (Braekke, 1983; Dang and Lieffers, 1989b; Pepin, Plamondon and Britel, 2002). Trees growing in peatlands, therefore, may be a suitable proxy for water-table level because of these relationships.

Studies which strive to understand the impact of water-table variability on tree growth have not yet investigated the distinct tree response to water-table level according to the microenvironment they inhabit in the wetland (topographic gradient and peat depth) (*e.g.*, Jean and Bouchard 1996; Smiljanić *et al.*, 2014; Cedro and Lamentowicz 2008). Past research has only assessed tree response between peatland trees and nearby dryer uplands (Linderholm, Moberg and Grudd, 2002; Cedro and Lamentowicz, 2011; Edvardsson *et al.*, 2015), and not between different locations within the peatlands themselves. Understanding the relationship between the proxy and the environment it inhabits is critical to accurately interpret these types of paleo-records (Hughes, Swetnam and Diaz, 2011). A research gap exists regarding the impact of water-table fluctuation and climate on tree-radial growth over long-time scales according to the locale they inhabit in the environment, such as the edge or the center of a peatland.

This study seeks to understand the role of peatland hydrology on the radial growth of eastern larch and black spruce trees growing in peatlands. Eastern larch and black spruce are a dominant tree species in the boreal forest of North America, which commonly inhabit peatlands (Sims, Kershaw and Wickware, 1990). Yet, both species radial-growth response to climate change in peatlands is poorly understood.

This manuscript seeks to answer the following three research questions: (i) Does water table affect eastern larch and black spruce radial-growth in a fen? I hypothesize that water-table level will be the main variable controlling eastern larch radial growth in the fen. This would be due to the species inhabiting the centre of the fen, where they are susceptible to increased hypoxic conditions. Correlation coefficients between eastern larch radial growth and water-table level will be higher than climate. Conversely, I hypothesize that black spruce radial growth will not indicate a significant relationship with water-table level. This is because black spruce is growing at the fen's edge, being less influenced directly by water-table variability, and its radial growth will be mostly driven directly by climatic variables. Correlation coefficients between black spruce radial growth and water-table level will not be significant and the species will present higher correlation coefficient values with climate parameters.

This chapter also seek to answer: (ii) Does the relationship between black spruce and eastern larch radial growth with peatland hydrology change over time? It was hypothesize that the relationship is not constant and it changes according to water-table level at the site due to changes in edaphic conditions, mainly related to oxygen availability and moisture conditions, negatively or positively influencing radial-tree growth in both species. Correlation values will indicate changes (positive or negative; higher or lower) according to specific water-table levels.

This research also strive to understand: (iii) is it possible to reconstruct water-table level from peatlands using tree-ring from eastern larch? It was hypothesize that eastern larch will be a suitable species to be used as a proxy to water-table level in peatlands as a result of the position it frequents within a fen ecosystem. Simulated water-table levels produced through the use of eastern-larch rings will indicate a good agreement with observed water-table levels for the site.

3.2 Material and methods

3.2.1 Study site

The details of the study sites are discussed in section 2.6 above (Chapter 2).

3.2.2 Climate and water-table level

3.2.2.1 Long-term data

High-resolution hourly-climate data is collected at BERMS sites. However, climate data is too short (1997 to 2016, 19 years) to conduct a reliable dendroclimatological analysis. Linear regression analyses were carried out between Prince Albert (PA) (station # 71869) and BERMS data to extend the temperature record back in time (Appendix A). Hourly/daily data were used to

develop monthly linear-regression equations, extending the temperature data from BERMS back to 1890. A set of equations was developed separately per site, OBS and FEN. The precipitation record was used directly from Waskesiu Lake (WL) (station # 71454). The monthly precipitation record from WL present high-correlation values to the BERMS sites ($r = 0.82$ – OJP; $r= 0.83$ – OBS, $p< 0.05$). All analyses were carried out using R software (R Core Team 2016).

The water-table data from the FEN site was provided by Environment Canada (Van der Kamp and Schmidt 2017) for the purpose of establishing radial-growth/water-table relationships. The water-table data was collected in the northern portion of the FEN, close to the study site. The record covered 9 years (2002 to 2011) and it was also necessary to extend the data in order to conduct a statistically valid dendrohydrological analysis. Regression analysis was again completed using daily-resolution historical water-level data from Waskesiu Lake (station #06CA002) and FEN water-table level data (https://wateroffice.ec.gc.ca). The water-table level of the FEN was reconstructed back to 1988.

3.2.2.2 Fine scale water-table level

To understand the water-table variability across the study area, three wells were installed in the three different microenvironments: the black spruce edge, the eastern larch inner edge, and the centre. Each well collected data every 15 minutes using a submersible pressure transducer (Solinst Levelogger; 0.05 psi accuracy) from August to October 2016. The data was corrected for barometric pressure (Solinst Barologger; 0.1cm accuracy). Statistical analyses were carried out between the three microsites to test for different variability in the water-table level in R (R Core Team 2016).

3.2.3 Site chronologies

To understand whether there is a different response between species growing in the FEN to water-table level, and whether this relationship changed according to the different micro-environments within the FEN (outer edge, inner edge and centre trees for both species), black spruce and eastern larch were sampled. Two cores were sampled from 20 black spruce trees growing at the edge (BSEF), 20 eastern larch trees growing at the inner edge (LAEF) and full cross sections of 20 eastern larch trees growing at the centre of the fen (LACF). The cores were extracted in the field using a 5.1 mmm increment borer, then stored in a plastic straw, and identified according to the species and microenvironment. Cross sections were sampled using a hand saw, trees were cut as low as possible to achieve the longest chronologies possible. The

samples were taken to the Mistik Askiwin Dendrochronology Lab, where they were processed. Extracted cores were glued into mounting boards, air dried, and cores and cross sections were sanded with progressively finer sandpaper: 80, 120, 220, 320, 400, 600 and 800 grit. Annual rings were then clearly visible under the microscope. Tree-radial growth was measured using a Velmex stage system and a 63X stereomicroscope with 0.001 mm precision (VoorTech, 2014).

The tree-ring series were statistically crossdated using COFECHA (Holmes 1983; Grissino-Mayer 2001). A 30-year segment with 15-year overlap was used to compare each series against a site-specific master chronology. This analysis calculated mean series inter-correlation (MSI) values, indicating how well correlated individual ring series are to their master chronology. The program also indicates potential crossdating problems, such as missing rings. Analyses were carried and series were re-measured if needed until the number of potential measurement issues were as close as possible to zero and the MSI value surpassed the 99% one-tailed confidence level (r=0.4226, 30-year segment). COFECHA also provides the chronology average-mean sensitivity value, which indicates how responsive the trees within the chronology are to their surrounding environment (Grissino-Mayer, 2001).

After crossdating, series were standardized using the program ARSTAN version 41d (Cook and Krusic 2006). The purpose of standardization was to eliminate inherent biological and age-related growth trends, achieving a better stand-level growth signal (Speer, 2010). A single detrending was carried out using a negative exponential curve. The negative exponential curve is considered to be a conservative technique because it fits the natural development of a tree growing in an environment without disturbance, presenting an exponential growth in the first years and declining through time. When the negative exponential curve did not fit a specific series, a horizontal line through the mean was applied. The program generates four different complementary chronologies, raw, standard, residual and ARSTAN chronologies (Speer 2010). In this research project, the standard chronology option was selected for all time series in the development of further analyses (Wettstein *et al.*, 2011). Standard chronologies are unit-less tree-ring indexes of growth over the annual-time series. The ring-index value indicates whether radial growth is above or below average. A ring-index value of one indicates average radial growth. A ring-index value greater than one indicates above-average radial growth, and a ring-index value less than one indicates below-average radial growth.

The expressed population signal (EPS) was assessed for each master chronology. The EPS measures the strength of the common stand-level signal that is dependent on the chronology sample depth (Speer, 2010). An EPS value above 0.85 is considered satisfactory and indicates that the common signal is composed of a representative number of individuals (Speer 2010). EPS is very important when using tree rings as a proxy for past climate, as values below 0.85 are deemed to be not suitable to represent the local environment (Speer, 2010). The EPS value was calculated using the package "dplR", in the R program (Bunn, 2008; Bunn and Korpela, 2015; Bunn *et al.*, 2015). An EPS value for every ten-year period was generated for each chronology (Appendix B).

3.2.4 Tree peatland chronologies as potential proxies

3.2.4.1 Tree growth predictors: climate and water-table level

Correlation function analyses were carried out between each master chronology, water-table level, and climate (temperature and precipitation) data on a monthly scale to assess the strength of tree-growth relationships to each variable. The function "dcc" in the Treeclim package (Zang and Biondi, 2015) in the R program (R Core Team, 2016) was used in this analysis. The function dcc calculates bootstrapped correlations, and the correlation coefficients are Pearson´s coefficients (Zang and Biondi, 2015). The significance level was chosen to be 95% in all climate analyses.

For the climate analysis, monthly temperature and precipitation were selected from previous-April to current-August as a predictor of radial-tree growth. To assess the relationship between water-table level and radial-tree growth, response function analyses were carried out using monthly water-table data from past-April to current-October as a predictor of tree growth against annual ring-width data from each master chronology (LACF, LAEF and BSEF) within the available water-table level window.

3.2.4.2 Moving correlation analysis

A moving correlation analysis was developed between monthly water-table data and annual radial-tree growth data, instead of using the entire data set (1988 to 2015) a 15, 20, and 25 -year moving window was applied. The analysis was developed using function dcc, but a "moving" setup was chosen for the item "correlation". The objective of this analysis was to determine whether radial-tree growth and the water-table relationship changed through time, and

so by using a moving average, long-term trends can be more easily uncovered. A moving average was calculated for the water-table data using the same 15, 20, and 25-year widow, to identify possible water-table thresholds that may have caused changes in short-term relationships.

3.2.4.3 Water-table reconstruction analysis

Water-table level was reconstructed through multiple linear regression analyses using the three master chronologies (BSEF, LAEF, LACF) in the R program (stats) (R Core Team, 2016). The reconstructions were developed during the 1940 to 2015 period, the common interval between all tree-ring chronologies. The best model was selected based on the Akaike´s Information Criterion (AIC) and the coefficient of determination (R^2) of the multiple linear regression. AIC is a numerical value used to rank competing models in terms of information loss in estimating reality (Burnham, Anderson and Huyvaert, 2011; Symonds and Moussalli, 2011). AIC´s objective is to achieve the most parsimonious and simplest model with the most explanatory power (Crawley, 2007). The model that presents the lower AIC value is considered the one that best approximates the process being predicted without overfitting (Burnham, Anderson and Huyvaert, 2011; Symonds and Moussalli, 2011). The best model was then cross-validated using the leave-one-out method (k=n) (Bengio and Grandvalet, 2004). Cross-validation analysis was carried out using function “cv.glm” in the R package boot (Canty and Ripley, 2017).

The hydroGOF package in R (Bigiarini, 2015) was used to calculate metric skills to validate the model, by comparing simulated and observed water-table level data. The parameters calculated are frequently used in the field of hydrological modeling and are indicated by this literature to evaluate the goodness-of-fit of the selected model (Legates and McCabe Jr., 1999; Moriasi *et al.*, 2007; Fry *et al.*, 2013). The explored metrics are: Pearson´s correlation coefficient (r), coefficient of determination (R^2), RMSE-observations standard deviation ratio (RSR), Nash-Sutcliffe efficiency (NSE) and percent bias (PBIAS). R^2 and r defines the degree of collinearity between observed and simulated data. The correlation coefficient ranges from -1 to 1, where r = 0 means that no linear correlation exists between observed and simulated; r= -1 indicates a perfect negative linear relationship, and r =1 indicates a perfect positive correlation. R^2 ranges from 0 to 1, describes the proportion of the variance in the observed data explained by the simulated data from the model. The NSE determines the magnitude of the residual variance

(noise) compared to the observed data variance. NSE ranges between ∞ to 1, where 1 indicates a perfect fit between the observed versus the simulated data. PBIAS measures the average tendency of simulated data to be larger or smaller than the observed data. RSR is a standardized version of the RMSE and combines the observed data standard deviation and an error index (See Appendix C).

3.3 Results

3.3.1 Water-table spatial variability

The fine scale water-table data collected in the three microsites studied (edge, inner edge and centre) were statistically analyzed to understand if the water-table level varies between the microsites sampled. The t-test analysis illustrated no statistical difference between microsites, therefore the water-table level seems to vary evenly throughout the areas of the FEN site tested (Appendix D).

3.3.2 Tree-ring chronologies

In total, five master chronologies were developed (Figure 3.1). Three master chronologies from the FEN: eastern larch chronology from the inner edge (LAEF), eastern larch chronology from the centre (LACF) and black spruce chronology from the edge (BSEF); and two master chronologies from the OBS: black spruce (BSO) and eastern larch (LAO). All chronologies had high MSI values (Table 3.1), above the established 99% confidence interval (Grissino-Mayer, 2001). The highest MSI value was from the LACF (0.696) and the lowest the LAEF (0.456). Eastern larch chronologies presented the highest AMS values, well above the 0.3, and therefore, are classified as sensitive (Grissino-Mayer, 2001). The black spruce chronologies presented lower AMS vales, indicating that the species is less responsive to the surrounding environment. The EPS values calculated for each master chronology were above the EPS value of 0.85, but some EPS values calculated per decade illustrated values below 0.85 (Appendix B).

Table 3. 1 FEN and OBS study site with the master chronologies information per site. BS = Black spruce; LA = Eastern larch; Number of cores = number of cores used to build the master chronology; Chronology Length = first year of growth – last year of growth (chronology age); Average Age of Trees = average age of trees composing the master chronology; EPS = expressed population signal; AMS = average mean sensitivity; MSI = mean inter-series correlation.

Site	Code	Species	Latitude	Longitude	Number of cores	Chronology Length	Average Age of Trees	EPS	AMS	MSI
FEN (Edge)	BSEF	BS	53°49.607'	104°37.354'	44	1903 - 2016 (114)	96.1	0.99	0.199	0.608
FEN (Edge)	LAEF	LA	53°49.571'	104°37.465'	39	1827 - 2016 (190)	122.6	0.97	0.427	0.456
FEN (Centre)	LACF	LA	53°49.536'	104°37.565'	38	1940 - 2016 (77)	50	0.96	0.477	0.696
OBS	BSO	BS	53°59.207'	105°06.973'	40	1889 - 2014 (126)	114.3	0.98	0.181	0.579
OBS	LAO	LA	53°98.729'	105°11.617'	39	1885 - 2016(131)	104	0.98	0.344	0.661

A cross-correlation matrix was built between master chronologies to demonstrate the dynamic relationship between each site and species (Table 3.2). The matrix presented no trends related to specific sites or species. The range of values (-0.068 to 0.632) demonstrated that some chronologies presented a similar growth response, while others were being driven by different factors or presented a different response to them.

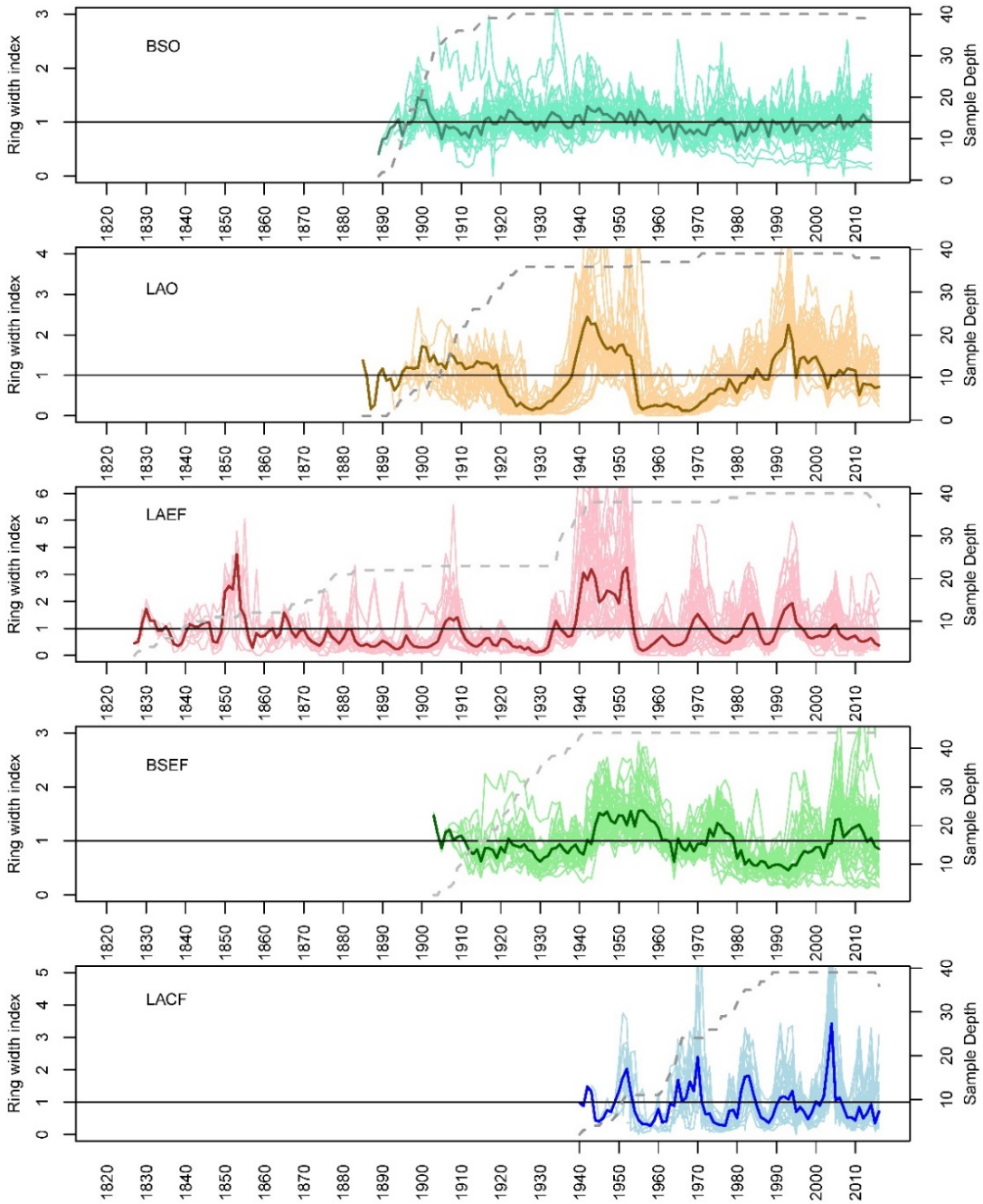

Figure 3. 1 FEN and OBS standard chronologies. The left y-axis is the ring width index (RWI), the right y-axis is the sample depth (number of increment cores), and the x-axis is years. The darker line represents the final master chronology, and the lighter lines represent the individual cores within each chronology. Above-average growth occurred in years when the master chronology is above the black horizontal line (RWI >1), and below-average growth when it is below (RWI < 1).

Table 3. 2 Cross-correlation matrix using the Pearson correlation coefficient, demonstrating the strength of the relationship between species and sites. Values in bold show significance above the 95% confidence interval.

Chronology	BSO	LAO	BSEF	LAEF	LACF
BSO	**1**				
LAO	**0.478**	**1**			
BSEF	**0.561**	**0.447**	**1**		
LAEF	0.383	**0.45**	0.395	**1**	
LACF	**0.504**	**0.46**	**0.486**	**0.48**	**1**

3.3.3 Climate correlation analysis

3.3.3.1 Trees in the FEN

The correlation function analysis between mean-monthly temperature and total-monthly precipitation with trees growing within the fen presented different results per species and per microsite (Appendix E). The BSEF revealed significant negative correlation between radial growth and past (year n-1) and current (year n) spring (May-June) temperature, and February (year n) temperature. Precipitation response function analysis did not indicate any relationship between BSEF radial growth and monthly precipitation. While, January (year n) precipitation indicated a positive relationship with LAEF radial growth. LAEF also presented a negative correlation to June temperature (year n-1 and year n). However, climatic variables were not able to explain any variability in the radial growth of trees growing in the center of the FEN (LACF).

3.3.3.2 Trees at OBS

Correlation functions analysis revealed a negative correlation between January (year n) precipitation and LAO (Appendix E). LAO also illustrated a negative correlation to June (year n) temperature, but positive correlation to April (year n-1). The BSO responded only to March (year n) temperature. The BSO presented a negative correlation between ring width and precipitation during winter (December, year n-1 and January, year n), at the beginning of spring (March; year n), and at the end of the growing season (August, year n).

3.3.4 Water table and tree-radial growth relationships

Correlation function analysis revealed a strong relationship between water table and radial-tree growth in the FEN (Figure 3.2). The analysis indicated that water-table level is the main driver of radial-tree growth in this environment. However, different species presented a contrasting relationship to the water-table variability. While the black spruce at the edge

presented a positive correlation to water-table level, eastern larch trees growing at the inner edge and in the centre of the fen presented a negative correlation to water-table level (Figure 3.2).

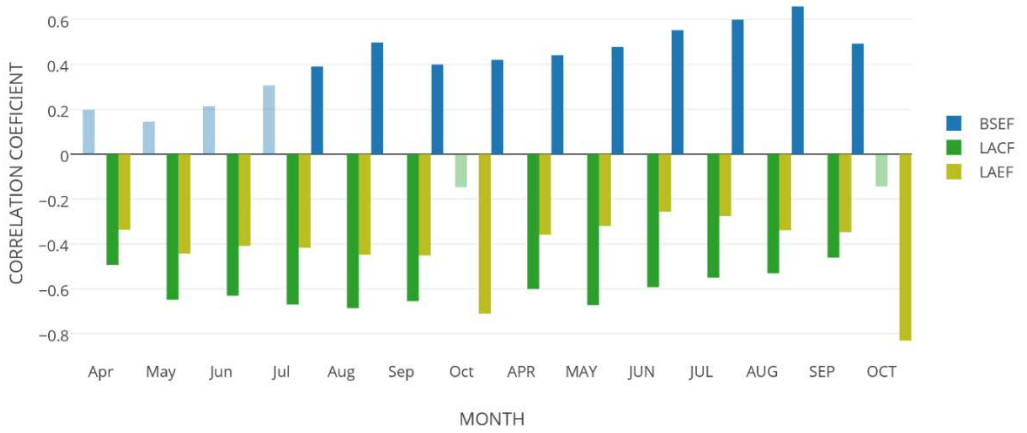

Figure 3. 2 FEN bootstrapped correlation function analysis (1988-2016) between standard master chronologies of BSEF (blue), LAEF (light green) and LACF (dark green) and water table. The 14-month period was examined from April to October of previous year and from April to October of current year. Lower case letters indicate months of the previous year, and upper case letters denote the current year's months. The darker bars are significant above the 95%confidence interval.

The BSEF ring widths illustrated a positive correlation to water-table level from the previous August (year n-1) to the current year September (year n). The current water-table level showed that it is more important than previous year´s water-table level to black spruce radial growth. The LAEF radial growth indicated a negative correlation to all months analyzed. Correlation function analysis in the centre of the FEN revealed significant correlation to all months analyzed, except October (year n-1 and year n). The LACF presented strong negative correlation values to water-table level in all months. Previous water-table levels is more important than current water-table level to eastern-larch radial growth.

3.3.5 Moving Correlation Analyses

3.3.5.1 Water-Table Level Threshold

The moving correlation analysis indicated water-table level threshold values that dictated changes in the relationship between radial-tree growth and water-table level in the FEN (Figure 3.3). The results of the 15-year moving average (half of a standard climatology) were selected to

represent this analysis in the Figure, for the other two long-term analyses (20 and 25-years) see Appendix F.

The eastern larch and black spruce radial growth illustrated periods of change in the temporal relationship to the water table, according to its level, and the period analyzed. The BSEF presented a negative relationship to water-table level (red) when the level was at its lowest point in the observed data (Figure 3.3, b; Table 3.3). However, when the water-table level rose (Figure 3.3, d), this relationship became positive (blue) (Figure 3.3, b). The LAEF also indicated specific periods of change in the relationship with the water-table level (Figure 3.3, c). Lower levels did not affect eastern larch radial growth at the edge of the FEN, however, when values rose above the lower-level period (below 487.72 m asl ± 0.03 m) the water table started to negatively affect radial-tree growth (red) (Figure 3.3 c, d; Table 3.3). With a continuous increase in water-table level, not only water-table values from previous, but also current growing seasons, started to affect LAEF radial growth (Figure 3.3 c, d; Table 3.3). In the centre of the fen, LACF radial-tree growth presented negative correlation (red) to water-table level during all periods analyzed (Figure 3.3, a). However, with an increase in the water-table level (Figure 3.3, d; Table 3.3), radial-tree growth was negatively affected by previous and current growing season water-table level in the FEN (Figure 3.3, a).

It is possible to observe specific periods where species present a change in the relationship with the water-table level. In general, changes observed through the moving correlation analysis occurred in a tight 8 cm zone between the 487.68 m asl and 487.76 m asl water-table level window, indicating the upper and lower threshold values for changes in water-table level that would affect radial-tree growth at the site (Table 3.3).\

Table 3. 3 Identified threshold values and periods of change in the relationship between water-table level and radial-tree growth (BSEF, LAEF, LACF). Shaded values indicate the upper (highest value) and lower (lowest value) water-table thresholds values for the site. Variation of these values was calculated to ± 0.03 m.

WTL Threshold (m asl)				
BSEF	487.68	(1991-2005)	487.73	(1995-2009)
LAEF	487.72	(1994-2008)	487.76	(1997-2011)
LACF	487.73	(1995-2009)		

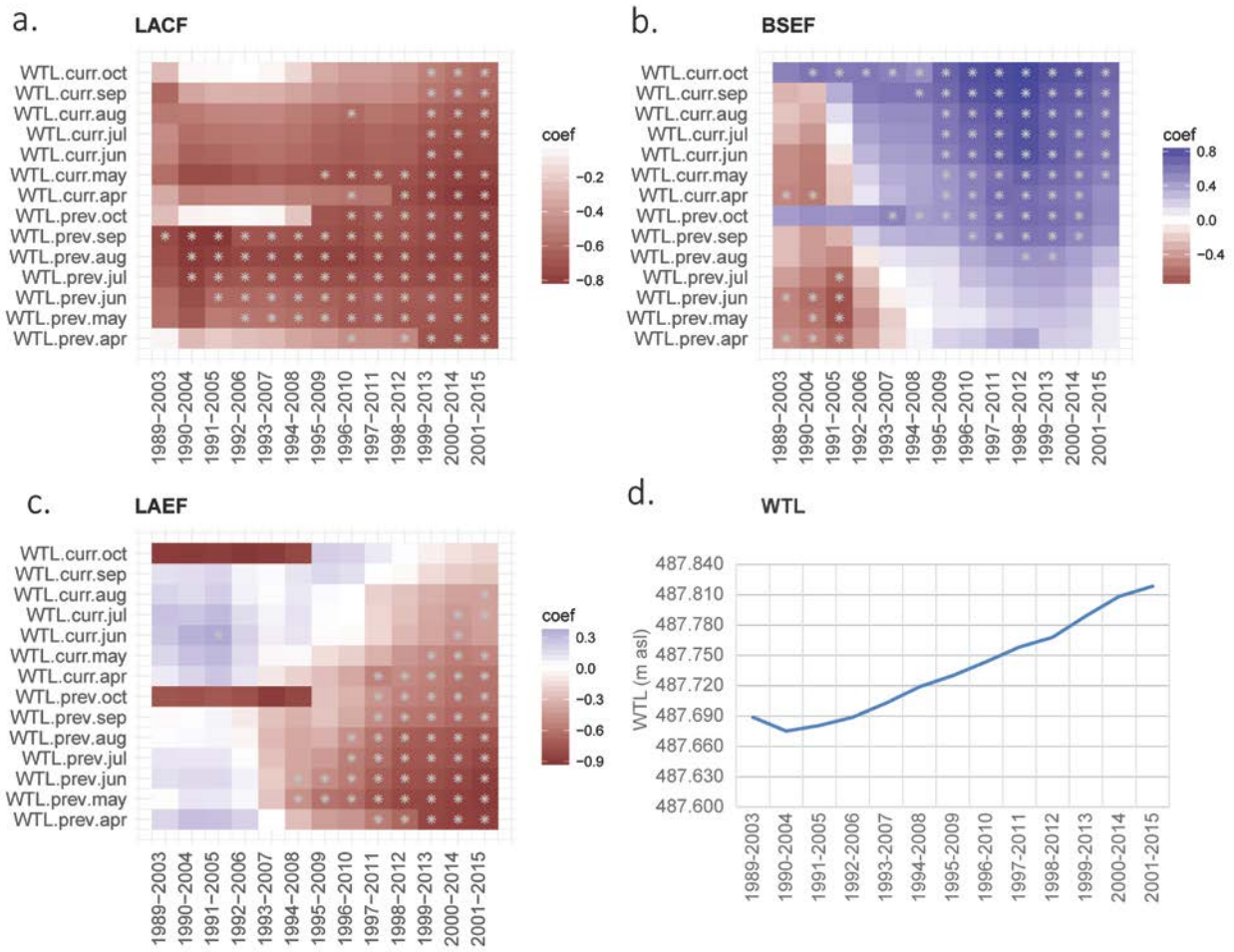

Figure 3. 3 Moving correlation analysis (15-year interval) (1989-2015) between standard master chronologies (LACF, LAEF, BSEF) and water-table level (15-year moving average interval) (WTL) in the FEN. Coef. = Correlation coefficients. Correlation coefficients indicated by an asterisk are significant above the 95% confidence interval.

3.3.6 Water-Table Level Reconstruction

Multiple-linear regression analyses were developed between the three chronologies: BSEF, LAEF, LACF (Appendix G). Chronologies were adjusted according to specific responses to water-table levels. The previous growing season (year n-1) presented the most explanatory power predicting LACF radial growth in the FEN. While for BSEF and LAEF, the correlation function analysis demonstrated higher correlations between radial-tree growth and current-year water-table levels (Figure 3.2). The model with the best goodness-of-fit described by AIC was composed of the LACF (previous year) and BSEF chronologies (current year) (AIC = -54.366; Figure 3.4). The model was evaluated using goodness-of-fit statistical metrics to assess the

accuracy of the simulated water-table level compared to observed water-table level (Figure 3.4). The cross-validation also indicated the good fitness of the selected model (MSE = 0.007).

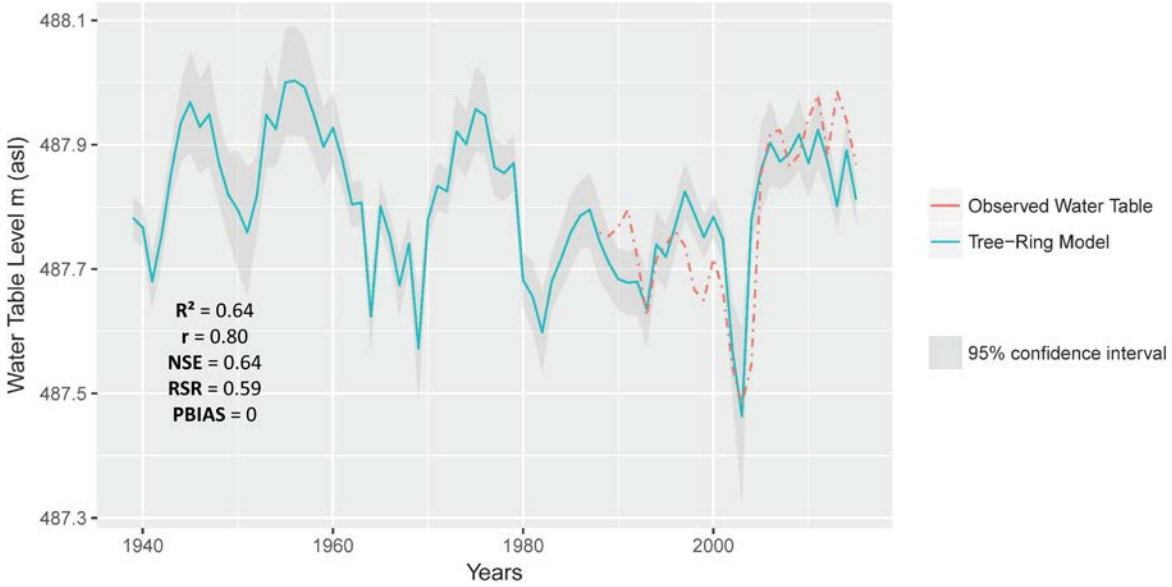

Figure 3. 4 Reconstructed water-table level from the fen using the tree-ring model. Observed water-table level in red, reconstructed water-table level in blue, and confidence interval for the reconstructed water-table level in gray.

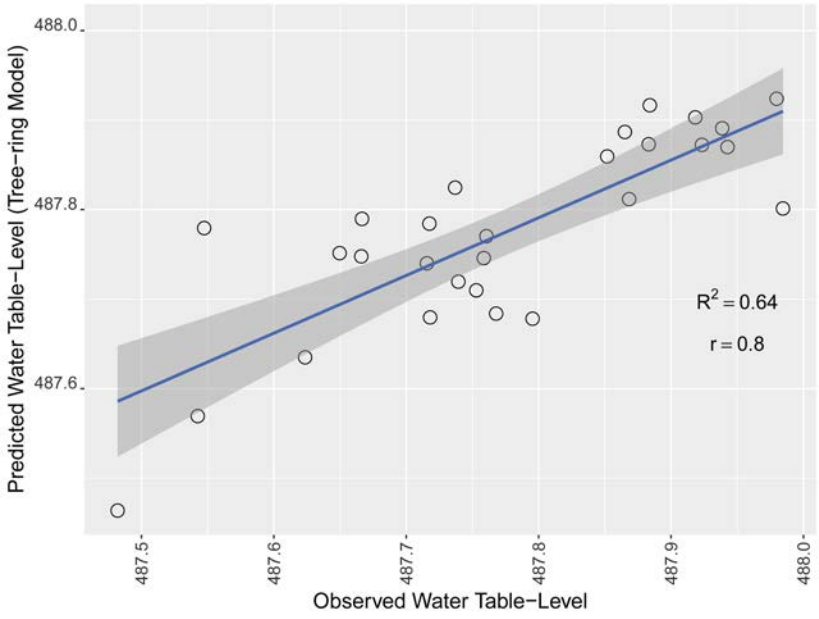

Figure 3. 5 Scatterplot of the observed water-table level and modeled annual water-table data. Regression line in blue and confidence interval in gray.

3.4. Discussion

3.4.1 Water table as the main driver of peatland trees growth

The lower correlation coefficient values observed between trees and climate in the FEN (Appendix E), but higher correlation values to water-table level (Figure 3.2), indicates that climate (precipitation and temperature) do not directly influence the radial growth of the trees in this specific environment. Instead, water-table fluctuations in response to long-term climate seems to be playing a more important role within this peatland ecosystems. This factor is consistent with other tree-ring studies conducted in European peatlands (Cedro and Lamentowicz, 2011; Dauškane, Brūmelis and Elferts, 2011; Smiljanić *et al.*, 2014; Edvardsson *et al.*, 2015).

However, eastern larch chronologies (LAEF and LACF) and black spruce (BSEF) revelead an opposite relationship to water-table levels in the fen (Figure 3.2). There is no evidence in the literature related to variability in growth responses between tree-ring chronologies within same peatland. Previous studies have only reported contrasting radial-tree growth between peatland trees and trees growing in the adjacent mineral substrate (Linderholm, Moberg and Grudd, 2002; Cedro and Lamentowicz, 2011; Edvardsson *et al.*, 2015). These studies illustrated a weak correlation between climate and peatlands trees, while trees growing on the mineral soil were significantly correlated to climate. The species investigated across the different substrates were the same, *P. sylvestris*. This is the first time that radial-growth variability was assessed across a gradient within the peatland and investigating more than one species.

3.4.2 Water table thresholds to radial-tree growth

Moving correlations analysis also indicated a differing relationship between tree rings and water-table levels through time (Figure 3.3). Analysis indicated shifts in the relationship between radial-tree growth and water-table level induced by alterations in water height (Figure 3.3; Table 3.3). However, the strength of this relationship (correlation coefficients, higher or lower values) and magnitude (positive or negative) is dictated by identified thresholds, which were found to be dependent upon species and microenvironment inhabited (Figure 3.3; Table 3.3). These results indicated that black spruce responds positively to increases in water-table level, whereas increases in water-table level negatively affects eastern larch, decreasing their radial-tree growth (Figure 3.3). There were periods where eastern larch chronologies indicated

distinct relationships to water-table levels. In periods of relatively low water-table levels (487.68-487.70 m asl; Figure 3.3 d), LACF showed a negative correlation to water table (Figure 3.3 a), while LAEF did not have any significant relationship to water-table level during the same period (Figure 3.3 c). Therefore, not only the species, but also micro-site conditions (topography and depth of peat), may be influencing the tree/water-table relationship. This is similar to what was discovered in a peatland rewetting event, where after 60 years of drainage and agricultural activity, approximately only 10 centimetres of difference in elevation influenced whether oak (*Quercus robur* L.) trees survived or died (Scharnweber *et al.*, 2015).

This distinct relationship between species and peatland hydrology described herein may be attributed to the species-specific physiological and morphological traits. Peatland trees are known to be affected by substrate oxygen depletion (hypoxic conditions), influencing root respiration, nutrient uptake, and mineral nutrition (Boggie 1972; Kozlowski 1982; Dang et al. 1991; Pepin et al. 2002). However, studies have indicated that eastern larch has adaptations to better tolerate root hypoxia (Islam and Macdonald, 2004; Calvo-Polanco, Señorans and Zwiazek, 2012), ensuring higher rates of root hydraulic conductance, and gas exchange to maintain physiological processes, that black spruce seems to lack (Islam, MacDonald and Zwiazek, 2003; Islam and Macdonald, 2004). Under long-term flood periods, plants decrease physiological activities such as nutrient uptake and growth (Kreuzwieser, Papadopoulou and Rennenberg, 2004) as consequence of a more energy demanding physiological processes (Kreuzwieser, Papadopoulou and Rennenberg, 2004; Ferner, 2009). This traits may explain the ability of eastern larch trees to inhabit the edge and centre of the site, while black spruce are limited to the edge. However, black spruce growing at the edge of the fen (more elevated site and shallower peat), become more vulnerable to a net lowering of the water table. Black spruce is considered a moisture sensitive species (Dang and Lieffers, 1989b; Huang *et al.*, 2009; Walker and Johnstone, 2014) and a lower level of water table, may induce moisture stress. A reduction in water availability in the peat surface seems to contribute to the reduction in stomatal conductance of the species that has a shallow root system (Strong and La Roi, 1983a; Lieffers and Rothwell, 1987; Pepin, Plamondon and Britel, 2002), affecting tree development, and carbohydrate assimilation for next year´s growth (Dang, Margolis and Collatz, 1998).

A fine-scale threshold was also indicated by the moving correlation analysis (Figure 3.3; Table 3.3). Minor alterations of only 8 cm changes to the water-table level can greatly affect the

relationship between peatland hydrology and radial-tree growth. To date no such study has been conducted that has identified water-table threshold levels to radial-tree growth in peatlands. The scale of change is consistent with studies investigating peatland gas exchange that indicated the existence of similar water-table thresholds to ecosystem respiration rates, and gross primary productivity changes accompanied with elevation-scales comparable to what was identified here. Silvola *et al.*, (1996) revealed an increase in CO_2 emissions after lowering of the water table by only 1cm, but reaching a saturation point at 30 to 40 cm below the former surface (Silvola *et al.*, 1996). Sulman *et al.*, (2009) studying wetland eddy covariance measurements of CO_2 identified an increase in 20 % of ecosystem production when water-table depth was located in a range between 5 and 35 cm below the surface. According to the authors, ecosystem respiration decreases with increase in water-table level above a similar critical-upper level.

3.4.3 Water table reconstruction

After comprehending the relationship between radial-tree growth and water-table level in the peatland, the possibility of reconstructing peatland hydrological variability was assessed. The multiple species tree-ring model illustrated a satisfactory good-fitness (Figure 3.4), suggesting that eastern larch and black spruce tree rings are a suitable proxy for water-table reconstruction. Results indicated a very good PBIAS (PBIAS < 10%) (Moriasi *et al.*, 2007; Fry *et al.*, 2013), a good RSR ($0.50 < RSR \leq 0.60$) (Moriasi *et al.*, 2007; Fry *et al.*, 2013) and a satisfactory NSE ($0.50 < NSE \leq 0.65$) (Moriasi *et al.*, 2007; Fry *et al.*, 2013). The two statistics describing the degree of collinearity between the observed and the model-simulated water-table levels indicated an agreement within data. The Pearson´s product-moment correlation coefficient (r) indicates a very good ($r \geq 0.8$) degree of collinearity between observed and simulated water-table level. The coefficient of determination (R^2) represented by the percentage of the portion of variance explained by the model (100% indicates a perfect model) (Razavi *et al.*, 2016) indicated that the model is able to explain 64% of the water-table variability in the period observed.

When compared to other dendrohydrological studies in the literature, the multiple tree-ring model performs well. For example, Smiljanić *et al.*, (2014) Scots pine model explained 55% of variability in water-table level in Central Estonia, 47 % and 71 % of groundwater variability was explained by Perez-Valdivia and Sauchyn (2011) in Alberta, 37 % and 43 % of streamflow was explained by Axelson *et al.*, (2009) model in South Saskatchewan, 42 % of streamflow was

explained by Urrutia *et al.*, (2011) model in Chile, and 62 % to 76 % was explained by the Woodhouse and Lukas (2006) tree-ring model in Colorado.

In addition, the model represented observed anomalies such as the drought of 2003 and the rise of the water-table level in 2011 and 2014. A more complex model developed in the White Gull Creek watershed using the Canadian Land Surface Scheme (CLASS) within the hydrologic–land surface modeling platform Modélisation Environmentale Communautaire (MEC)–Surface and Hydrology (MESH) was used to characterize streamflow (Davison *et al.*, 2016). This model, though robust in its own right, failed to predict the 2011 flood (Davison *et al.*, 2016). Despite the difference in magnitude between stream flow and water table, the White Gull Creek recharges the FEN and because of that a comparison is possible. This illustrates the point that the use of more complex models does not always achieve better results, and that the use of a simpler model, such as the one developed in this research, can be effective. Specifically because the use of simple models makes it easier to characterize uncertainty when compared to more complex models (Davison *et al.*, 2016). Moreover, tree rings can be tested directly against instrumental records of the predicted variable which makes easier to characterize the relationship between them, as well as to decrease uncertainty (Charman *et al.*, 2004; Elshorbagy *et al.*, 2016). This research also introduced the opportunity to advance in boreal hydrological process-based model by better understanding the complex relationship between the species specific response to peatland hydrology. The better understanding of plant community interactions with hydrological changes can help to advance in the parameterization of those land-surface properties and reduce model uncertainty (Gong *et al.*, 2012).

The strength of this tree-ring model largely originates from the use of multiple species with opposite responses to water-table level and located in different microsites within the same fen. Together, these factors contribute complimentary data outputs to better reconstruct the hydrology of the peatland. The model is not relying on just one biological response and physiological strategy of a single species, but instead two, and both from different microsites within the fen environment. This approach advantageously introduces the opportunity of validating the model by comparing each species response to the instrumental hydrological record. To date, the use of eastern larch and black spruce to reconstruct water-table level in peatlands in Canada has not been explored and no other reconstruction of Canadian peatlands have been developed to make further comparisons.

3.5 Conclusion

Dendrohydrological assessments of tree-ring responses to peatland hydrological variability within a boreal Saskatchewan fen suggest that water-table level is the main factor driving radial-tree growth in this environment. In contrast with what was first hypothesized, black spruce illustrated weak correlations to climate, but strong correlations to water-table level as what was expected only with eastern larch radial growth.

As previously hypothesized, the relationship between radial-tree growth and water-table level is not constant over time. Alterations in water table dictates changes in the relationship between peatland hydrology and tree growth. Hydrological thresholds identified specific changes in radial-tree growth accompanied with shifts above and below the thresholds. These alterations, showed that small changes in water-table level, above or below these threshold values, have large implications in the growing environment, potentially leading to shifts in species composition that drive important successional processes in peatland ecosystems (Laine, Vasander and Laiho, 1995; Weltzin *et al.*, 2003; Talbot *et al.*, 2010). A change in environments created by a rise or fall in peatland hydrology could lead to the dominance of one species over the other, or create an unsuitable environment to both species to grow within these peatlands ecosystems. Because an opposite relationship between these specific species was discovered to water-table level, in the future, fine-scale change in water-table level may be an important warning signal of a more broad scale vulnerability of treed peatlands to ongoing climate change. This is specifically because changes in plant species composition, and peatland hydrology, have already been shown to greatly affect a peatland's capacity to store carbon and water.

The annual ring-width of trees growing in the fen showed themselves to be suitable proxies to water-table levels in this environment. This result was only somewhat consistent with the earlier-stated hypothesis. Eastern larch annual radial-tree growth was found to vary with water-table level as theorized, but black spruce tree-ring widths also carried with water-table level and were very good at contributing to a model to reconstruct past water-table level in the fen. Long-term water-table observations can therefore provide a better understanding of the sensitivity and vulnerability of peatland hydrology to climate change through these types of proxy relationships. Since long-term hydrological data is overall quite scarce, the use of a model to reconstruct water-table level variability is very useful in the environments that black spruce and eastern larch inhabit.

CHAPTER 4: UNDERSTANDING THE INFLUENCE OF PEATLAND HYDROLOGY ON LARCH SAWFLY (*Pristiphora erichsonii* (Hartig) OUTBREAKS

4.1 Abstract

Insect outbreaks are a major forest disturbance in the boreal forest in Canada. Reconstructing previous outbreaks are crucial to understanding natural factors that lead to insect defoliation periods, improving our ability to predict future infestations and increasing the reliability of forest management plans and pest control programs. Researchers have often been limited in their ability to draw accurate conclusions regarding the history of larch sawfly (*Pristiphora erichsonii* (Hartig) outbreaks in North America. It is well known that floods can affect survival of larch sawfly populations, as well as suppress radial growth of eastern larch (*Larix laricina* (Du Roi) K. Koch) trees. Eastern larch often inhabits peatlands where high water-table levels can lead to a decrease in tree-ring widths. Water-table level suppressions result in similar radial-growth patterns to when trees are defoliated by larch sawfly, making accurate diagnoses of larch sawfly outbreak a challenge. This fact becomes more accentuated when non-host species used for standard dendroecological outbreak analyses (often black spruce (*Picea mariana* (Mill.) Britton) present an opposite relationship to water-table variability, enhancing chances of drawing erroneous outbreak conclusions.

This paper introduces a novel approach to advance the reconstruction of larch sawfly history. It stresses the necessity of using long-term hydrological analyses to accurately infer outbreak periods to distinguish them from times of water-table suppression. In this study, five outbreaks where identified using a traditional outbreak analysis (1903-1911, 1916-1936, 1953-1966, 1973- 1979, and 2002- 2016). However, the last outbreak was found to be a result of hydrological growth suppression and not sawfly defoliation. Observations indicated that periods of low water-table level may lead to the incidence of larch sawfly in northern Saskatchewan.

This study draws attention to the importance of improving analyses regarding larch sawfly outbreaks and introduces insights regarding hydrological effects on insect cycles in peatlands.

4.2 Introduction

Tree rings have been broadly used to reconstruct past climates (e.g., Gray *et al.*, 2007; Stahle *et al.*, 2007; Hughes *et al.*, 2011) and to investigate ecological disturbances, such as fires (*e.g.*, Niklasson and Granstrom 2000; Monson, 2003; Oris *et al.*, 2014), and the history of insect outbreaks (*e.g.*, Girardin *et al.*, 2001; Case and Macdonald 2003; Taylor *et al.*, 2006; Nishimura and Laroque 2010; Speer *et al.*, 2016). Insect outbreaks can cause severe damage to forest ecosystems, dramatically reducing their ability to provide ecosystem services (Schowalter, 2012; Dhar, Parrott and Heckbert, 2016).

Larch sawfly (*Pristiphora erichsonii* (Hartig)) is an important defoliator in North America (Ives, 1976), with the principal host for this insect being the eastern larch (*Larix laricina* (Du Roi) K. Koch) (Lejeune and Hildahl, 1954; Lejeune, Fell and Burbidge, 1955; Tailleux and Cloutier, 1993; Jardon, Filion and Conrad, 1994). Trees infested by the insect respond to defoliation by decreasing needle production in an attempt to prevent an increase in insect population density (Lejeune, Fell and Burbidge, 1955). Also, recurrent defoliations can lead to tree population mortality (Graham 1956), while nonfatal infestations result in an intense reduction in radial growth within the trees (Ives and Nairn 1966a; Bergeron *et al.*, 2002).

Outbreak periods can be identified and reconstructed using tree-ring chronologies (Jardon, Filion and Conrad, 1994; Liang, Filion and Cournoyer, 1997). A specific benefit of tree-ring reconstruction is that it provides the proper temporal resolution for assessing insect population outbreak cycles characterized by long intervals (Speer 2001; Speer *et al.*, 2016). The outbreak is identified in the form of radial-growth depressions (Graham, 1956). Specifically, larch sawfly outbreaks are normally characterized by the presence of a pale latewood in the annual ring during the year that the infestation occurs, followed by a decrease in radial growth and an increased incidence of missing or locally absent rings during subsequent years (Jardon, Filion and Conrad, 1994; Girardin, Tardif and Bergeron, 2001; Case and Macdonald, 2003; Girardin *et al.*, 2005; Nishimura and Laroque, 2010). Growth suppression signature periods can last from four to nine years after a severe outbreak (Nairn *et al.*, 1962; Girardin *et al.*, 2005).

Larch sawfly larvae emerge from May to July and lay their eggs in young terminal shoots of eastern larch (Lejeune, Fell and Burbidge, 1955). Larvae feed on the foliage, causing severe

damage to the tree's needles and greatly reduce their capacity to actively photosynthesize. From July to August, when the larvae are fully developed, they move out of the trees to the ground, spinning cocoons, and spending approximately the next 10 months on the ground before reaching adulthood (Lejeune, Fell and Burbidge, 1955). During this phase on the forest floor, flooding can decimate larvae populations (Lejeune and Filuk, 1947). In peatland environments, such as bogs and fens, larch sawfly outbreaks occur at lower intensities and duration because this specific forest-floor habitat restricts the development and survival of the larvae during typical wet springs (Lejeune, Fell and Burbidge, 1955; Graham, 1956; Ives and Nairn 1966b; Ives, 1976).

In Canada, larch sawfly outbreaks have been documented since the late nineteenth century (Ives and Muldrew, 1984). In Western Canada, historical records indicate that the first outbreak, described as high intensity, occurred from 1908 to 1915 in Manitoba and Saskatchewan (Lejeune and Martin 1948; Nairn *et al.*, 1962). In 1954, a survey carried out in the Prince Albert and Waskesiu Lake areas of Saskatchewan provided evidence of larch sawfly outbreaks in the early 1950s (Lejeune and Hildahl, 1954). Prince Albert National Park's eastern larch chronologies presented a high incidence of missing rings and the presence of light rings, which were associated with specific larch sawfly outbreaks (Case and Macdonald, 2003).

Although it is critical to understand the insect cycle and distribution, dendrochronological studies of larch sawfly outbreaks in Saskatchewan are limited (*e.g.*, Nairn *et al.*, 1962; Case and Macdonald 2003). The presence of sawflies can lead to a weakened response of radial-tree growth to climate (Girardin, Tardif and Bergeron, 2001; Case and Macdonald, 2003; Girardin *et al.*, 2005), which can make it difficult to reconstruct past climates during the period of outbreaks. To explore the use of tree rings as a proxy for climate reconstruction and to understand the impact of the larch sawfly on eastern larch growth in Saskatchewan, the above limited network of chronologies needs to be extended.

To date, no study has compared water-table variability in peatlands during larch sawfly infestation cycles. As demonstrated by the few European dendrohydrological studies conducted in peatlands, water-table level is the main environmental factor controlling radial-tree growth in this environment (Cedro and Lamentowicz, 2011; Dauškane, Brūmelis and Elferts, 2011; Smiljanić *et al.*, 2014). This result was also shown in a peatland in Saskatchewan, where eastern larch and black spruce radial growth was limited by water table-variability at a fen site (Chapter 3). Changes in water-table level can result in growth depression and an increase in incidence of

missing rings, mimicking the tree's response to larch sawfly outbreaks within their ring patterns. Also, not all larch sawfly events are represented by a pale ring, which can make it even more challenging to distinguish the source of suppression (Girardin *et al.*, 2005; Nishimura and Laroque, 2010). Water-table variability can also impact the establishment of the larch sawfly populations due its flood sensitive phase on the forest floor (Lejeune, Fell and Burbidge, 1955; Graham, 1956; Ives and Naim 1966b; Ives, 1976). Since populations of eastern larch in the prairie provinces mostly inhabit peatland habitats (Nairn *et al.*, 1962), it is important to distinguish larch sawfly growth suppression from changes in water-table levels in order to appropriately reconstruct past larch sawfly histories. It is also begs the question whether water-table levels and larch sawfly cycles are linked, since site hydrology has been shown to be important on larvae development (Lejeune, Fell and Burbidge, 1955).

I seek to reconstruct larch sawfly outbreaks in northern Saskatchewan at two sites with distinct hydric regimes. Specifically, I focus on the following research question: i) Are larch sawfly outbreaks influenced by water-table variability in peatlands? I hypothesize that larch sawfly outbreaks are influenced by the site hydrology. Years of water-table drawdown will benefit the development and establishment of the insect at a site, inducing outbreaks. Without better knowledge of what is driving larch sawfly cycles, predicting future outbreaks may remain very difficult.

4.3 Material and Methods

4.3.1 Sites description

The details of the sites for this study are described in detail in section 2.6 above (Chapter 2).

4.3.*2 Chronologies development*

The co-occurring species with eastern larch at both sites was black spruce, and therefore it was selected to be the non-host species. Healthy black spruce trees were sampled on the edge of the FEN. At OBS, black spruce was found well distributed across the area, and it was randomly sampled across a one hectare plot. At the FEN, two eastern larch chronologies were developed. The first chronology was developed using trees growing on the inner edge, within the shallower peat zone, and the second chronology was developed using eastern larch from the centre of the fen in the deeper peat zone. These two chronologies made up of the same species,

but from adjacent micro-environments, helped to determine if the tree-ring patterns contained different outbreak intensity signals. Master chronology development is described in section 3.2.3 above (Chapter 3).

4.3.3 Identification of anomalous rings

Visual identification of possible wood anatomical characteristics associated with outbreak periods was conducted when building the chronologies, according to the criteria already established in the literature; (1) the occurrence of a pale latewood ring in the initial year of defoliation; (2) a following decrease in radial growth, and; (3) an increase in the presence of incomplete and missing rings. This procedure is seen as a the most standardized outbreak methodology according to the literature record (Harper, 1913; Girardin, Tardif and Bergeron, 2001; Case and Macdonald, 2003; Girardin *et al.*, 2005; Nishimura and Laroque, 2010).

Pale latewood rings are characterized by a thin wall of latewood cells that appear lighter than the latewood cells of other rings (Girardin *et al.*, 2005). These cells are easily visualized under a microscope, and the pale rings are usually followed by a period of suppression of radial growth (Figure 4.1). Larch sawfly larvae damage eastern larch trees by feeding from current foliage and defoliating large areas in successive years (Graham, 1956). After successive years of defoliation, eastern larch trees reduce the amount of foliage produced, which contributes to a reduction of radial growth and increases the incidence of locally absent and missing rings in those periods (Harper 1913; Graham 1965; Girardin et al. 2005). These characteristics allow for the identification of larch sawfly signals within the chronologies.

4.3.4 OUTBREAK analysis

To accurately identify larch sawfly outbreaks in the study sites, a host/non-host analysis was conducted using the program OUTBREAK version 1.50P (*c.f.*, Case and Macdonald, 2003; Girardin *et al.*, 2005; Nishimura and Laroque, 2010). Separate analyses were conducted for each eastern larch chronology, at each site. OUTBREAK analyses help to identify suppression growth periods in the host that are absent in the non-host species in the same period (Holmes and Swetnam 1996). To conduct these analyses, both species have to present a similar growth-climate response (Swetnam *et al.*, 1985), so that small rings produced due to climatic effects are not misread as due to sawfly defoliations. In our sites, eastern larch chronologies were compared to black spruce chronologies growing at the same site. Black spruce have already been used in the literature to help to identify larch sawfly outbreaks within eastern larch (Girardin, Tardif and

Bergeron, 2001; Case and Macdonald, 2003; Girardin *et al.*, 2005; Nishimura and Laroque, 2010).

Potential larch sawfly outbreaks were detected when depressions in the host chronology lasted for at least four years and where the maximum growth reduction in the suppression period reached a threshold value of 1.28 standard deviations below the mean ring-width value (Speer *et al.*, 2001). These threshold parameters selected for the present study follow similar larch sawfly parameters already established in the literature (Girardin, Tardif and Bergeron, 2001; Case and Macdonald, 2003; Girardin *et al.*, 2005).

For this study, I classified outbreak periods as either; 1) major - for when the number of trees affected are equal to or greater than 2/3 of those sampled at the site (relative frequency ≥ 66%); 2) medium – for when the number of trees affected are between 2/3 and 1/3 (≤ 66% relative frequency but ≥ 33%), or; 3) minor - for when the number of trees affected are equal or less than 1/3 (relative frequency ≤ 33%) of those sampled at the site.

4.3.5 Larch sawfly outbreak analysis using peatland hydrology

In this FEN, the water-table level is the most important factor controlling radial growth of black spruce and eastern larch (Chapter 3). However, black spruce radial growth is positively correlated to a rise the water-table level, while the eastern larch is negatively correlated to the same parameter (Chapter 3). Therefore, an increase in water-table level in the FEN results in an increase in radial growth for black spruce, but in a decrease in radial growth for eastern larch (Chapter 3) . An OUTBREAK analysis of this data would therefore interpret high water-table level periods as a growth suppression in the host species, and will therefore indicate it as a larch sawfly defoliation event if it surpasses the 1.28 standard deviation. Since the program does not distinguish between a growth suppression event induced by a change in water-table level from that of a larch sawfly outbreak period, all previous studies using these two species may include a potential serious flaw in their analyses, depending on the exact locations of the water-table level at each study site (Girardin, Tardif and Bergeron, 2001; Case and Macdonald, 2003; Girardin *et al.*, 2005; Nishimura and Laroque, 2010). The use of another non-host chronology could solve the problem, but in this case, as with most sites in previous studies, there is no other tree species present at the same sites except black spruce to use.

OUTBREAK results were evaluated against the reconstructed water-table level at the fen study site. The goal of this analysis was to identify any trend in the water-table level that would

have led to an outbreak, since the insect development is dependent in flood free periods (Lejeune, Fell and Burbidge, 1955). Water-table threshold values previously identified as key (lower: 487.68 m asl ± 0.03; upper: 487.76 m asl ± 0.03) to radial-tree growth dynamics at the site (Chapter 3), and the long-term average (487.81 m asl ± 0.03) was used to set low, high, and average water-table levels in the study.

4.4 Results

4.4.1 Chronologies

In total, five chronologies were developed. Three chronologies were from FEN: two eastern larch chronologies, one from the edge (LAEF) and one from the center (LACF) and one black spruce chronology (BSEF) from the edge of the fen. Two additional chronologies were constructed from OBS: one eastern larch chronology (LAO), and one back spruce chronology (BSO) (Table 4.1). A cross-correlation matrix was developed between master chronologies to demonstrate the dynamic relationships between the sites and species (Table 4.2).

Table 4. 1 FEN and OBS study site with the master chronologies information per site. BS = Black spruce; LA = Eastern larch; N° of cores = number of cores used to build the master chronology; Chronology Length = first year of growth – last year of growth (chronology age); Aver. Age of Trees = average age of trees composing the master chronology; EPS = expressed population signal; AMS = average mean sensitivity; MSI = mean inter-series correlation.

Site	Code	Species	Latitude	Longitude	Number of cores	Chronology Length	Average Age of Trees	EPS	AMS	MSI
FEN (Edge)	BSEF	BS	53°49.607'	104°37.354'	44	1903 - 2016 (114)	96.1	0.99	0.199	0.608
FEN (Edge)	LAEF	LA	53°49.571'	104°37.465'	39	1827 - 2016 (190)	122.6	0.97	0.427	0.456
FEN (Centre)	LACF	LA	53°49.536'	104°37.565'	38	1940 - 2016 (77)	50	0.96	0.477	0.696
OBS	BSO	BS	53°59.207'	105°06.973'	40	1889 - 2014 (126)	114.3	0.98	0.181	0.579
OBS	LAO	LA	53°98.729'	105°11.617'	39	1885 - 2016(131)	104	0.98	0.344	0.661

Table 4. 2 Cross-correlation matrix using the Pearson correlation coefficient, demonstrating the strength of the relationship between species and sites. Values highlighted in gray indicate significance above the 95% confidence interval.

Chronology	BSO	LAO	BSEF	LAEF	LACF
BSO	**1**				
LAO	**0.478**	**1**			
BSEF	**0.561**	**0.447**	**1**		
LAEF	0.383	**0.45**	0.395	**1**	
LACF	**0.504**	**0.46**	**0.486**	**0.48**	**1**

4.4.2 Larch sawfly outbreaks

Visual identification of larch sawfly tree-growth suppression and the occurrence of pale rings were carried out using a microscope. Pale latewood rings were identified in 65 of 120 eastern larch cores (54.2%); all were followed by growth suppression periods. The incidence of pale latewood rings could have been greater if the sample depth during the 1950´s period had been greater in the center of the fen. In all cases, a pale incomplete ring was characterized by a faded latewood portion (Figure 4.1). Pale rings occurred the most often in 1953 and 1954. In some cores, pale rings also re-occurred between 1961 and 1966, and during the late 1920s (from 1915 to 1925). Three to nine narrow rings characterized the period of suppression after a pale ring was found. In some trees, the presence of locally absent rings were also observed.

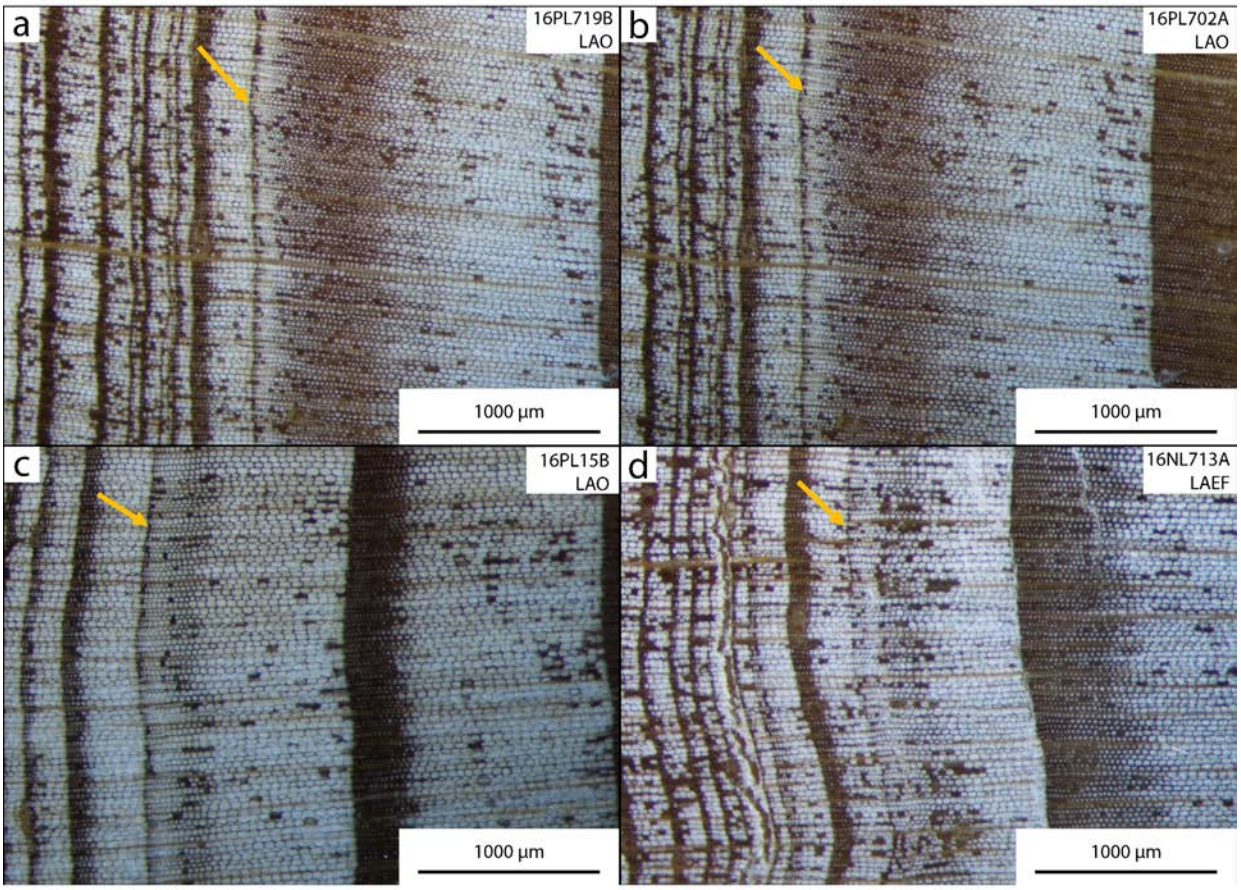

Figure 4. 1 The image shows characteristics of larch sawfly outbreaks in eastern larch chronologies. a. The upper arrow indicates the pale latewood ring, followed by a period of growth suppression in the OBS (LAO); b. the arrow points to the pale latewood ring and a subsequent decrease in radial growth in the OBS (LAO); c. a latewood ring is present in the image pointed by yellow arrow in the OBS (LAO); d. the arrow points to the pale latewood ring and a subsequent decrease in radial growth in the FEN (LAEF).

Growth depression periods could be visually identified in the eastern larch chronology (LAO) from OBS when compared to the black spruce chronology (BSO) occurring at the OBS site from 1919 to 1936 and from 1953 to 1978 (Figure 4.2). Growth suppression periods could also be identified in the eastern larch chronology at the edge of the FEN from 1953 to 1962 and 2006 to 2016 (Figure 4.2) and in the center of the FEN from 1954 to 1963 and 1971 to 1978 (Figure 4. 2). Together, the visually identified periods of growth suppression illustrated a synchronicity with the presence of the pale latewood ring.

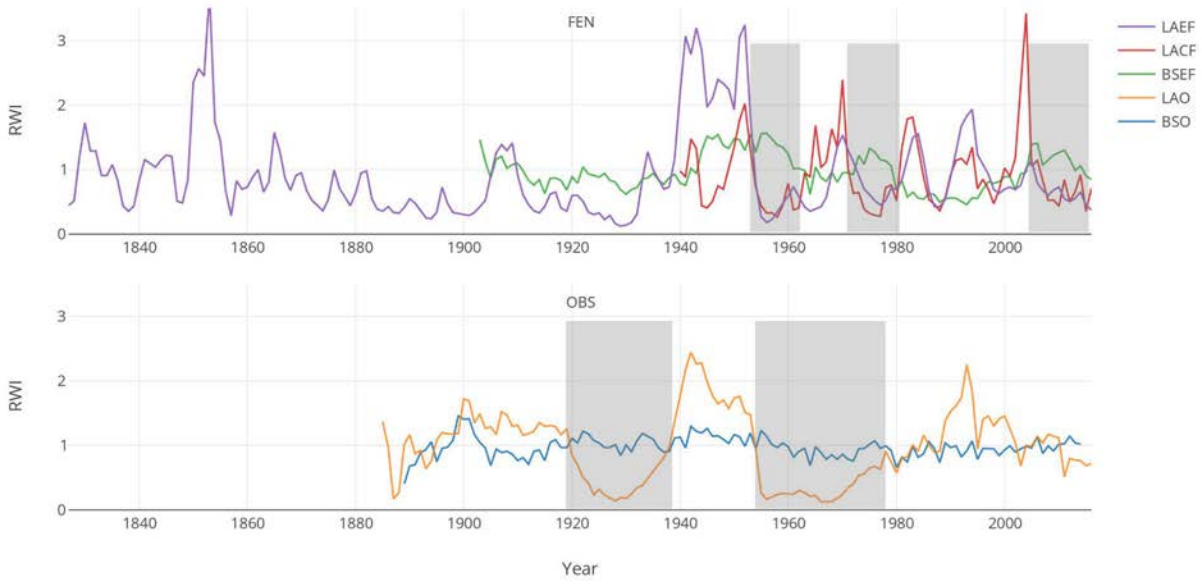

Figure 4. 2 Tree-ring chronologies from FEN and OBS site, respectively. Gray blocks are indicating suppression periods.

4.4.3 OUTBREAK analysis

The host/non-host analysis with the OUTBREAK program revealed significant and synchronous outbreak periods between sites (Figure 4.3). At the OBS site, there were two major outbreaks identified, from 1920 to 1936 and from 1953 to 1963. In the FEN, the LAEF chronology contained two major outbreaks periods, from 1953 to 1966 and 2001 to 2016, and two medium outbreaks from 1903 to 1912 and 1973 to 1979. The LACF chronology indicated two major outbreaks, from 1953 to 1962 and 2004 to 2016, and one medium outbreak 1971 to 1979. Minor outbreaks were defined, but it was not deemed important for this analysis. The

majority of years identified with a minor outbreak occurred prior or after a major or medium period (Figure 4.3).

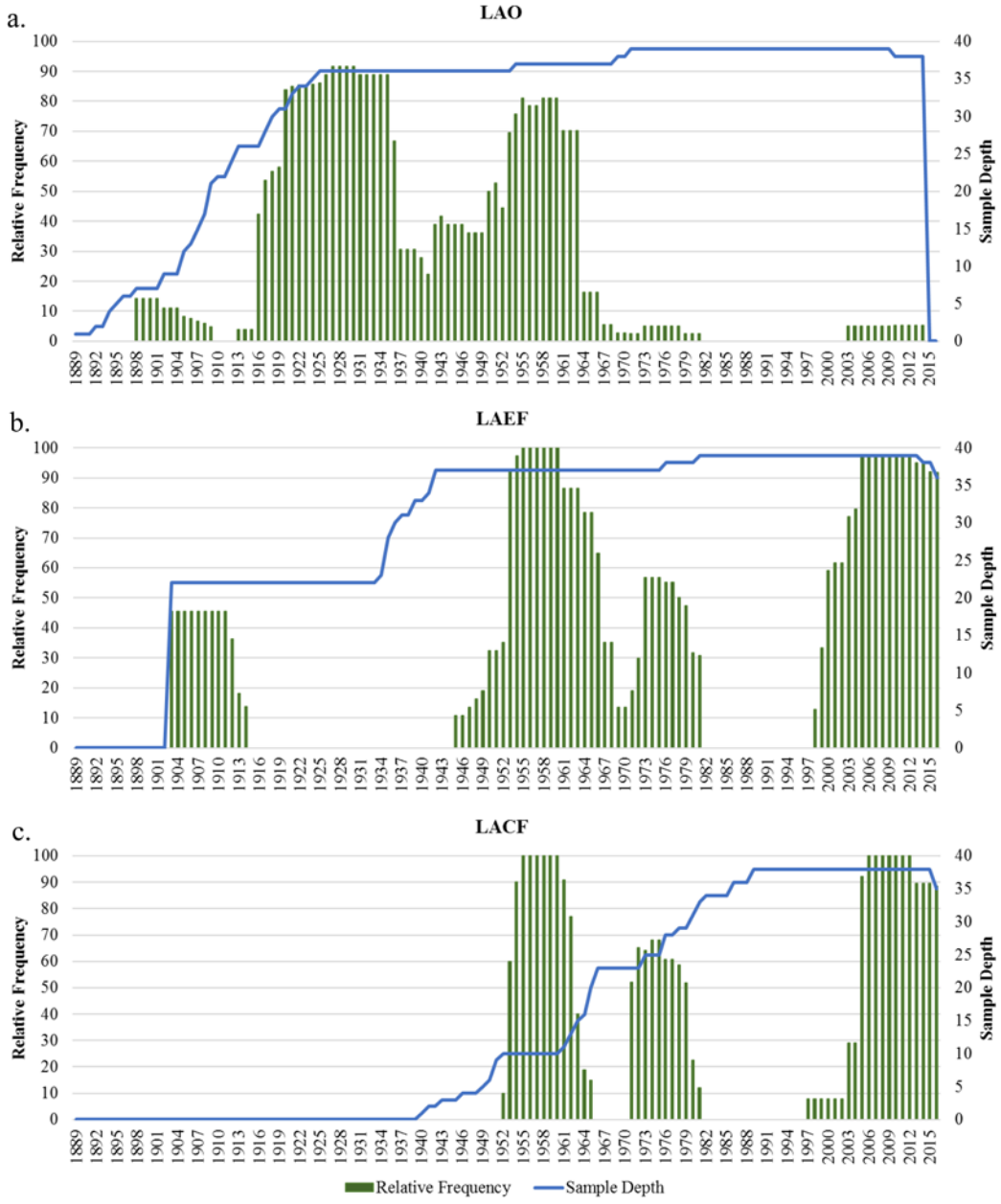

Figure 4. 3 Percentage of eastern larch series affected by larch sawfly (green), by year, with sample depth (blue). A). LAO chronology in the OBS; B). LAEF chronology in the FEN; C) LACF chronology in the FEN.

OBS and FEN sites showed one major outbreak periods that overlapped, from 1953 to 1962. The larch sawfly defoliation affected 90.7% of the trees on the edge of the FEN, 91.7% of the trees in the center, and 76% of the trees at the OBS site (Figure 4.3). While the outbreak lasted for 11 years at OBS, it lasted for 14 years at FEN (Figure 4.3). The other major and medium outbreaks that occurred at FEN (1903-1912, 1972-1979 and 2004-2016) only appear as minor outbreaks at the OBS site.

4.4.3 Larch sawfly outbreak and peatland hydrology

The OUTBREAK results were compared against a long-term water-table record for the site (Figure 4.4) (Nehemy 2017). Since this proxy record only dates back to 1940, relationships between outbreak events and the water-table level were not analyzed prior to this period. Before the major outbreak of 1953 (1948 to 1952), the water-table level was low and in a decreasing trend since 1945. This decreasing trend in the water-table level lasted for seven years (1945 to 1951) (Figure 4.4). It then reached, and rose above the upper threshold value before the outbreak period in 1952.

The second drop in the water-table level started in 1964, when the water-table level dropped below the lower-threshold value. From 1964 to 1970 (7 years) the water-table level was varying between upper threshold and lower threshold (Figure 4.4). After 1970, the OUTBREAK analysis indicated a growth suppression period from 1971 to 1979 for LACF and from 1973 to 1979 for LAEF. Outbreaks occurred with higher frequency in the first two years in the center compared to the edge, which increased above 50% in 1973. The third outbreak period (2002 – 2016) also presented with a short dry period before its initiation. However, it did not last as long as the previous drier phases described. The water-table level only started to drop below the upper threshold value in 2001 and recovered in 2004 (Figure 4.4).

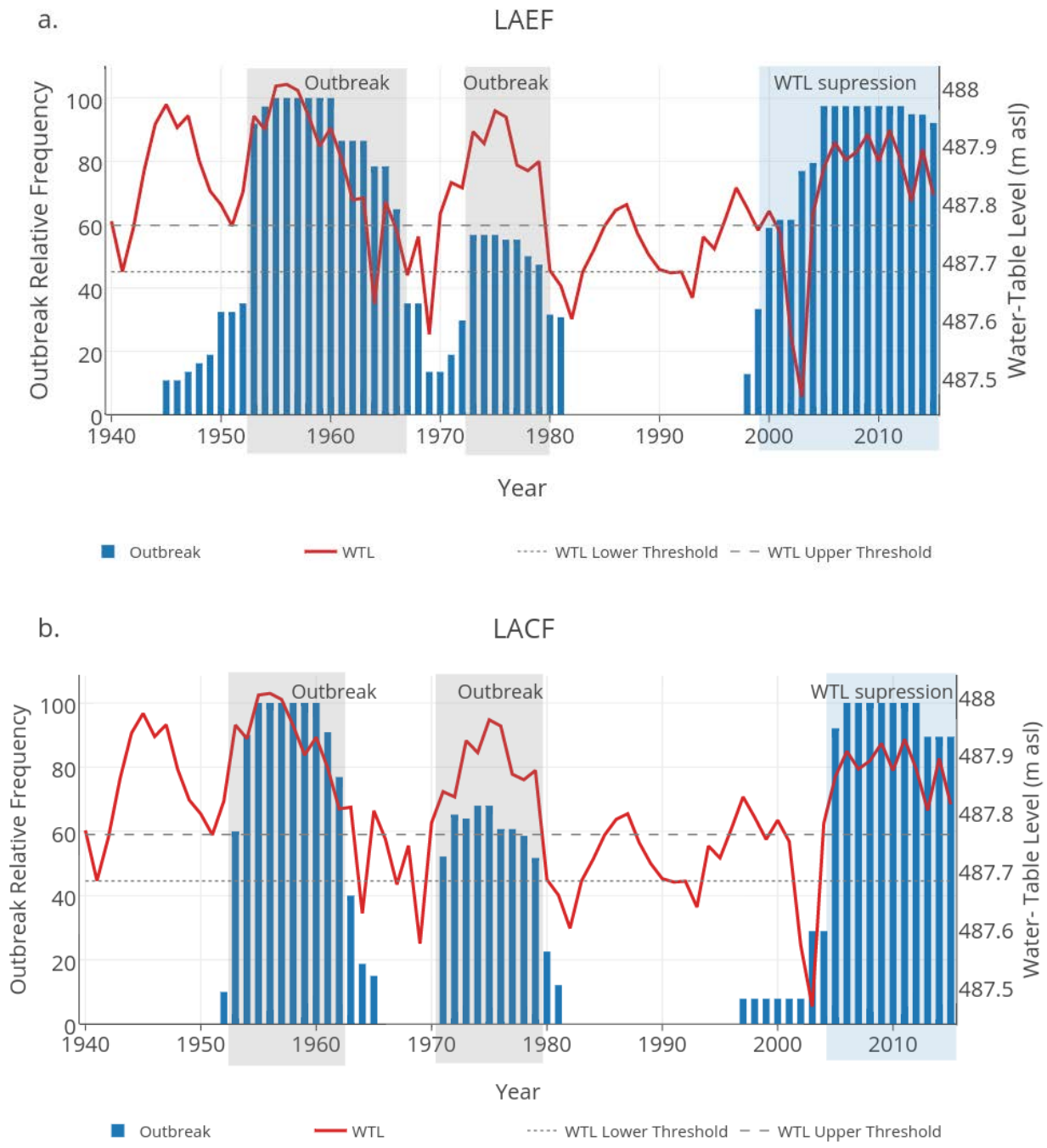

Figure 4. 4 Percentage of eastern larch series affected by larch sawfly (blue), by year, with reconstructed water-table level (red) and threshold levels (dashed line). A). Analysis developed for LAEF; B) analysis developed for LACF in the FEN.

Table 4. 3 Table comparing results from previous reconstructions of larch sawfly outbreaks in Canada with results from the current study. Filled windows indicate that the period overlap to the current study outbreak period, while empty (white) periods indicate periods that do not overlap.

Authors	Before 1895	1895 -1915	1916 -1936	1937-1957	1958 - 1978	After 1979
Current Study		**1903-1912**	**1920-1936**	**1953-1966**	**1972-1977**	
Nishimura & Laroqque 2010 (NL)		1891-1919	1927-1950	1954-1970	1976 - 1985	
Girardin et al. 2005 (MB)	1891-1892	1903-1912		1959-1964		
Case & MacDonald 2003 (SK)	1891-1893	1901-1906	1922-1927	1953-1959	1973-1979	
Girardin et al. 2001 (QC)	1891-1894	1895-1912		1955-1962		
Jardon et al. 1994 (QC)	1884-1906	1907-1911		1938-1952		1984-1989
Arquilliere et al. 1990 (QC)		1905-1908		1940-1946		
Nairn et al. 1962 (SK and MB)		1908- 1919	1924-1927	1938-1959		
Lejeune & Hildahl 1954 (SK ans MB)				1945-1953		

4.5 Discussion

4.5.1 Growth suppression

The time periods defined by the OUTBREAK analysis, supported the pale ring and suppression periods defined by the anatomical analysis. In total, five major outbreak periods were identified in both sites (Figure 4.3). These events occurred from 1903-1911, 1916-1936, 1953-1966, 1973-1979, and 2002 -2016. OBS and FEN had outbreak periods that overlapped (Figure 4.3), with the only difference being two outbreaks occurring in the FEN (LAEF and LACF) from 1972 to 1979 and the mostly recent outbreak from 2004 to 2016, that appear of very low frequency at OBS site (Figure 4.3). Considering all outbreak periods analyzed between sites, outbreaks were shown to be of greater intensity in the FEN (the site mostly influenced by hydrological regimes) than in the OBS, which contradicts the previous indications in the literature (Lejeune, 1955; Graham, 1956; Ives and Nairn, 1966b; Ives, 1976). In this case, this difference between relative frequencies between sites may not be a consequence of the influence of hydric regimes that imposes the development and survival of the insect, instead it may be a consequence of canopy cover. In the OBS the canopy is dominated by black spruce with sparsely disperse eastern larch trees covering around 10% of the canopy in the site (Barr *et al.*, 2012), which may not have provide enough resources and the insect may have concentrated the population in stands more dominated by eastern larch.

The timing of outbreaks periods identified in this study coincides with larch sawfly events already reported in the literature (Table 4.3). The first outbreak identified in this study (1903-1911) perfectly overlapped the outbreak reported by Girardin *et al.*, (2005) in sub-Arctic Manitoba (Table 4.3). In Waskesiu Lake, Saskatchewan, a larch sawfly defoliation period was identified from 1901 to 1906 (Case and Macdonald 2003), overlapping three years with the

period found in the BERMS. Nairn et al. (1962), studying larch sawfly in Manitoba and Saskatchewan, reported an event from 1908 to 1919, also supporting the evidence of larch sawfly in the period observed in our sites. This outbreak was also reported in eastern Canada (Table 4.3). Jardon *et al*., (1994) described occurrence in northern Quebec, Girardin *et al.*, (2001) in Lake Duparquet, southern Quebec, Arquillière *et al*., (1990) in subartic Quebec and Nishimura and Laroque (2010) In Labrador (Table 4.3).

The second outbreak identified (1920-1936) occurred at the OBS, but it was not identified in the FEN. The outbreak may not have occurred in the FEN as a consequence of high-water table periods and not creating an opportunity for the establishment of the larch sawfly that need flood free periods to stablish and develop (Lejeune, Fell and Burbidge, 1955). Unfortunately, the water-table records for this site do not cover this period. This outbreak was, however, reported by Case and Macdonald (2003) in Saskatchewan (Table 4.3). The growth suppression caused by larch sawfly at Waskesiu Lake only lasted five years, from 1922 to 1927, while at the OBS site, it lasted for 16 years. Other dendroecological studies also reported an outbreak overlapping the period here described (Nairn *et al.*, 1962; Nishimura and Laroque, 2010) (Table 4.3).

The third outbreak (1953 to 1966) occurred at a higher frequency in the OBS and FEN. According to Nairn et al. (1962), the earliest larch sawfly of endemic proportions in central Manitoba and Saskatchewan started in 1941, reaching a climax around 1951 to 1953, and losing intensity around 1955. The authors also reported that before this period, there were few records of tree mortality caused by larch sawfly in the western provinces of Canada. In Saskatchewan, larch sawfly outbreaks were reported from 1945 to 1954 (Lejeune and Hildahl, 1954). This report was made in 1954 when larch sawfly defoliation was still happening in Manitoba and Saskatchewan. Also, in central Manitoba and Saskatchewan, defoliation caused by larch sawfly was identified from 1938 to 1959 (Nairn *et al.*, 1962). In Waskesiu Lake, Saskatchewan, depression periods in tree growth were identified from 1953 to 1959. In the Churchill Manitoba, area, Girardin et al. (2005) reported growth suppression caused by larch sawfly from 1959 to 1964. In eastern Canada this outbreak was also reported (Table 4.3).

The fourth outbreak identified in this study (1973 to 1979) only occurred in the FEN, in the OBS it was insignificant (only 5% relative frequency). It may be related to the opportunity created by the low water-table level in the period prior to the outbreak, allowing the development

and establishment of larch sawfly in a drier peat environment (Figure 4.4). This outbreak was also identified in the most studies analyzed in the field (Table 4.3). Case and Macdonald (2003) identified growth suppressions occurring in the same period (1972 to 1977) at Waskesiu Lake. Nishimura and Laroque (2010) also reported an event that coincides with the same period, but the event lasted for a longer period (1976-1985) (Table 4.3).

Only the latest outbreak, from 2002 to 2016, was not identified in any study reported in the literature analyzed (Table 4.3). I believe that this last outbreak identified by OUTBREAK analysis may not be a growth suppression caused by larch sawfly defoliation, but instead a water-table level issue with the non-host species analysis (see discussions below).

4.5.2 Larch sawfly cycle relationship to hydric regimes

Different insect outbreaks in forest environments have been shown to rely on seasonal patterns of moisture variability often related to patterns of interannual and interdecadal climatic variation (Hebertson and Jenkins, 2008; Marcias Fauria and Johnson, 2009; Sherriff, Berg and Miller, 2011).In this study, I investigated the possible influence of peatland hydrology on larch sawfly outbreak, not previously investigated in the literature. The comparison analysis between larch sawfly outbreak frequency generated by standard OUTBREAK analysis and the long term site water-table data indicate a dependence of larch sawfly to peatland annual hydrological regime (Figure 4.4).

Long periods of low water-table levels in the FEN may have promoted the establishment of larch sawfly populations at a site, resulting in subsequent growth suppression in the following years (Figure 4.4). This theory is supported by the flood-free periods that larch sawfly populations need to complete their cocoon cycle at ground-level (Lejeune, Fell and Burbidge, 1955). During the larch sawfly cycle, fully developed larvae drop to the ground in July and August, burrowing in the moss or forest floor and spinning cocoons to spend the next 10 months or more at ground level (Lejeune, Fell and Burbidge, 1955). In the spring, from May to June, the insects likely resume their development in cocoons and become adults. Prolonged flooding at ground level during the cocoon phase causes severe mortality of larch sawfly populations (Lejeune, Fell and Burbidge, 1955).

We also observed that after the drought period in both earlier outbreaks identified, there was a period during which the water-table level was high (Figure 4.4) but did not decimate the larch sawfly population, and defoliation persisted for the next years. This phenomenon could be

explained by the fact that not all larch sawfly stages in cocoons are susceptible to flooding (Lejeune, Fell and Burbidge, 1955). According to the authors, cocoons in the diapause stage are highly resistant to flooding. And, cocoons under water do not present any further development, which may indicate that insects in diapause remained in that stage until favorable conditions emerge. Also, about 25% of the cocooned larvae remain in the ground for a prolonged diapause, spending two or more winters in this phase (Lejeune, Fell and Burbidge, 1955). These observations presented in the literature may indicated that non-synchronized phases within the entire insect population may favor the persistence of the larch sawfly at a site even when average-annual water-tables levels are high.

In the last outbreak indicated by host/non-host analysis (2002-2006), unlike the other two periods observed where the water-table level was gradually dropping and established for couple years, it had only three years of low water-table level (Figure 4.3). This short period may not have been sufficient to establish larch sawfly populations at the site. Additional support for the water-table level growth suppression hypothesis is the lack of evidence in the literature and provincial forestry records about larch sawfly outbreaks in the last 20 years. Also, upon visiting the FEN site in 2016 there was no visual evidence of larch sawfly outbreak in the site (personal observation).Therefore, it may have been a consequence of the different growth response to hight water-table level between eastern larch and black spruce observed for the site (Nehemy 2017). A water-table level above upper threshold produces a wider than average ring in the non-host species (BSEF) and a small than average in the host (LACF and LAEF) (Figure 4.2), and therefore a widening of the difference in the host/non-host relationship past the threshold level in program OUTBREAK (Figure 4.4).

The theory that larch sawfly populations attack eastern larch in the FEN after a relative long drought period is also consistent with the drought stress theory (White, 1976; Mattson and Haack, 1987). Increases in air temperature can benefit insect populations by improving their reproductive capacity and growth rates (Mattson and Haack, 1987). Periods of low water-table level in the FEN (more likely to be warmer and drier) may have benefited larch sawfly populations. It is also believed that stressful conditions increase plant vulnerability to insect herbivory (White, 1976; Mattson and Haack, 1987). First years of outbreak incidence are followed by increase in water-table level above upper threshold level (Figure 4.4) which are known to cause growth suppression in eastern larch in the site as result of hypoxic conditions

(Nehemy 2017), which may have increased eastern larch vulnerability to outbreak, benefiting sawfly population.

4.5.3 Tree-ring chronologies

All five chronologies developed contain a significant inter-series correlation r-value, well above the minimum required value of 0.4226 for significance at the 99% confidence interval based on a 30-year overlapping segment (Grissino-Mayer, 2001) (Table 4.1). The highest inter-series correlation was 0.696 from the chronology of eastern larch trees in the center of the FEN, and the lowest was 0.456 from the eastern larch chronology at the edge of the FEN. As expected, the average mean sensitivity of all eastern larch chronologies was higher than the average mean sensitivity of any black spruce chronology. The longest chronology was from eastern larch at the edge of the fen, reaching 190 years in age, and the shortest was from the eastern larch growing in the center of the fen, that were only 77-years old.

The Cross-correlation matrix presented no trends related to specific sites or species (Table 4.2). The range of values (-0.068 to 0.632) demonstrated that some chronologies presented a similar growth response, while others were being driven by different limiting factors or presented a different response to them. The eastern larch growing at the edge of the FEN and the eastern larch growing in the OBS presented the highest inter-series correlation ($r = 0.632$), indicating a similar growth response to the local environment. The correlation value between the two black spruce master chronologies was the second highest value in the matrix ($r = 0.475$), also pointing to the presence of a similar limiting factor of radial growth at both sites. The correlation between black spruce and eastern larch at OBS was shown to be significant. However, the black spruce chronology (BSEF) and the larch chronologies from the centre (LACF) of the FEN did not show a significant correlation. The BSEF chronology illustrated a significant correlation to the eastern larch growing in the edge (LAEF). In the FEN, there was a greater correlation between the same species ($r=0.359$) than between different species (0.184), which was expected.

4.6 Conclusion

This study provided further evidence of the history of larch sawfly in the province of Saskatchewan, Canada. The three eastern larch chronologies studies from both sites presented synchronicity in relation to periods of growth suppression caused by larch sawfly defoliation. The visual identification of pale latewood helped to identify periods of growth depression and

were synchronized to larch sawfly incidence. The host/non-host analysis indicated that larch sawfly activity in central Saskatchewan aligned to outbreaks periods from other provinces in Canada. The four main periods identified were: 1903-1912, 1920-1936, 1953-1966 and 1972-1977. The results also provided evidence that low intensity outbreaks do not always occur at more hydric sites, it could also be dependent in other factors.

More importantly our results substantiate a better understanding of the influence of hydrology on larch sawfly occurrences in peatlands, providing additional insight into larch sawfly outbreak cycles. Prolonged periods of low water-table levels may assist in leading to an insect outbreak. Based on the observations made, it is recommended that an analysis of long-term hydrological variability of the site should also be taken in consideration when identifying periods of larch sawfly. Outbreak analysis will be made with higher accuracy, decreasing the uncertainty related to potential growth suppression sources (hydric regime or insect defoliators).

These findings may have greater relevance considering predicted climate change. Increases in drought periods may potentially increase the vulnerability of the eastern larch population to larch sawfly defoliation in peatlands. Additional research is needed to better understand whether this pattern is also found in other sites and whether there is a major climatic patterns driving those outbreaks. It is also essential to stress that the evidence of correlation with relative short-time series and descriptive analyses are not by themselves sufficient evidence to infer causality of the associations here described. However, identifying climatic variations and the relationship to forest disturbances is essential to a better understanding of ecological processes and the improvement of proper forest management strategies (Dale *et al.*, 2001; McKenzie *et al.*, 2004).

CHAPTER5: CONCLUSION

5.1 Summary of findings and final considerations

In this thesis, the radial-tree growth of eastern larch and black spruce response to peatland hydrology and larch sawfly outbreak in a Saskatchewan peatland (FEN) was explored. It also assessed radial-tree growth response of both species in a drier site (OBS) as reference. In total five tree-ring chronologies were developed (BSEF, LAEF, LACF, LAO, BSO) and used for analysis.

Prior to this thesis, there were no long-term water-table reconstructions in peatlands using tree-rings in Canada (Chapter 3). This study introduced this topic by advancing our understanding of the relationship between radial-tree growth of (black spruce and eastern larch) and peatland hydrology. Analysis was completed for a relatively long-term water-table record using tree chronologies derived from three microsites with two different tree species in a moderately-rich fen in order to determine the impact of water-table variability within the this peatland ecosystem. Dendrohydrological analysis demonstrated that the water-table level is the main factor driving eastern larch and black spruce radial growth in peatlands. The results showed high correlation coefficients between monthly water-table level and annual ring width. This finding indicates the suitability of both species as a natural proxy for assessing long term water-table variability

Interestingly, correlation function analysis also illustrated that the species have an opposite relationship to water-table level. Black spruce trees inhabiting the edge of the FEN increase radial growth with a rise of the water-table level, showing a positive correlation. Conversely, eastern larch growing in the edge and centre of the site indicated a negative correlation to water table, showing a decrease in ring width with the increase in the level of the water table. The relationship observed here is hypothesized to be a result of a combination of the

species morphological and physiological traits, leading to habitat selection within the peatland, and a response to this microenvironment. Prior to this study, literature has only indicated different growth behaviors between peatland and upland trees as a result of different variables (*e.g.,* temperature) which control radial-tree growth.

Further, I identified threshold levels that dictate changes in the relationship between radial-tree growth and water-table level at the site. Upper and lower thresholds demonstrated that fine-scale variability in the water-table level in peatlands can result in drastic changes in ring-width. Prolonged changes in the hydrology at the site above - or below-established thresholds could potentially lead to shifts in plant species composition. These findings reinforce the importance of the hydrological regime in controlling plant species composition in peatlands. Additionally, this observations brings to light the sensitivity of forest communities in peatlands to predicted climate change. With future changes in the hydrology of this environment, as a consequence of predicted increase in temperature and evapotranspiration, shifts in plant species communities can occur. Changes in plant species composition and density has a large potential to alter peatland carbon storage capacity and hydrological characteristics.

After assessing specific species radial responses to water-table variability, a tree-ring model was developed using both species to reconstruct past water-table level. The tree-ring model outcome was classified as satisfactory and provided a longer term perspective of the hydrological variability at the FEN site. Long-term hydrological data contains sufficient hydrological variability to promote a better understanding of climate impacts and interaction within the hydrology of peatlands.

Advances in the understanding of peatland tree species dynamics and introducing the opportunity to reconstruct peatland hydrology with a fine-temporal resolution (annual scale) can provide guidelines for future research that aims to restore peatlands in Canada. To encourage the establishment of desired tree species in the system, my research illustrates the importance to monitor the variability of water-table level.

In this thesis, I also introduced the opportunity to advance larch sawfly outbreak analysis in Canada and to identify future outbreaks (Chapter 4). It is well known that the majority of eastern larch communities in Canada inhabit peatland ecosystems, where the species radial growth responds negatively to high water-table levels, but also negatively to larch sawfly defoliation. Both stressors can result in growth depression periods creating similar patterns in

eastern larch ring sequences. Previous studies have pointed to this problem, and because of it, an accurate identification of outbreak periods have not been successfully achieved. To improve this analysis, I compared long-term hydrological records with larch sawfly outbreak analysis. I identified periods where the water-table level gradually dropped and remained below average for at least five years, leading to an outbreak occurrence. This hypothesis is also supported by the insect's dependence on flood free periods. Between the five outbreak periods identified in the study site using established outbreak analysis (host/non-host species), one of them was a false positive outbreak, as the suppression was a result of high water-table levels. The host/non-host analysis misinterpreted this data due to the different responses between the eastern latch and black spruce species to water-table variability. The high water table at the site promoted an increase in black spruce radial growth, and a decrease in eastern larch radial growth. Previous studies that were situated in sites highly influenced by hydric regimes could have misinterpreted such events as a larch sawfly outbreak due to the lack of hydrological data and knowledge about the different behaviors between host and non-host species within the hydrologically influenced microhabitat.

Advancing out knowledge regarding larch sawfly population dynamics and factors that lead to outbreaks can improve forest management practices and pest management programs. Further, it is recognized that climate change is going to increase forest disturbances in boreal ecosystems. Insect defoliation is a major disturbance in the boreal biome, therefore improving forest managers understanding about insect population cycles and their interaction with the environment is crucial to increase predictability and mitigate forest degradation.

5.2 Limitations and future research opportunities

This thesis illustrated the importance of fine-scale variability in peatland hydrology to the survival and growth of tree species as well as the importance of introducing hydrological variability when analyzing larch sawfly outbreaks in peatlands. A broader-scale analysis using more study sites would bring more confidence to the results presented here, and could open opportunities to introduce other factors that may not have been observed in my studies, such as fire disturbances. The length of the reconstructed-water table also limited the outbreak analysis. Increasing the length of the chronologies would improve our analysis by adding more outbreak periods to be observed against the known hydrological data records. However, it opened more opportunities to future research to explore larch sawfly outbreak relationships with hydrological

periods never discussed before in the literature. Long-term climatological patterns (*e.g.*, PDO, AMO) may also be influencing this patterns observed here, therefore exploring this relationship may also contribute to advance the knowledge in peatland ecosystem dynamics.

The new knowledge about the suitability of both peatland tree species to reconstruct water-table level introduced allow us to further explore it. From a paloeclimatogy and paleohydrology perspective, it would be interesting to investigate whether subfossil peatland trees of eastern larch and black spruce present the same relationship with hydrology indicated by the live trees. And, if possible, extend the chronologies back in time to achieve a longer-term hydrological data for the site. It would create opportunities to understand the long-term climate/hydrology relationship and possibly assess anthropogenic influence of climate and hydrology through time.

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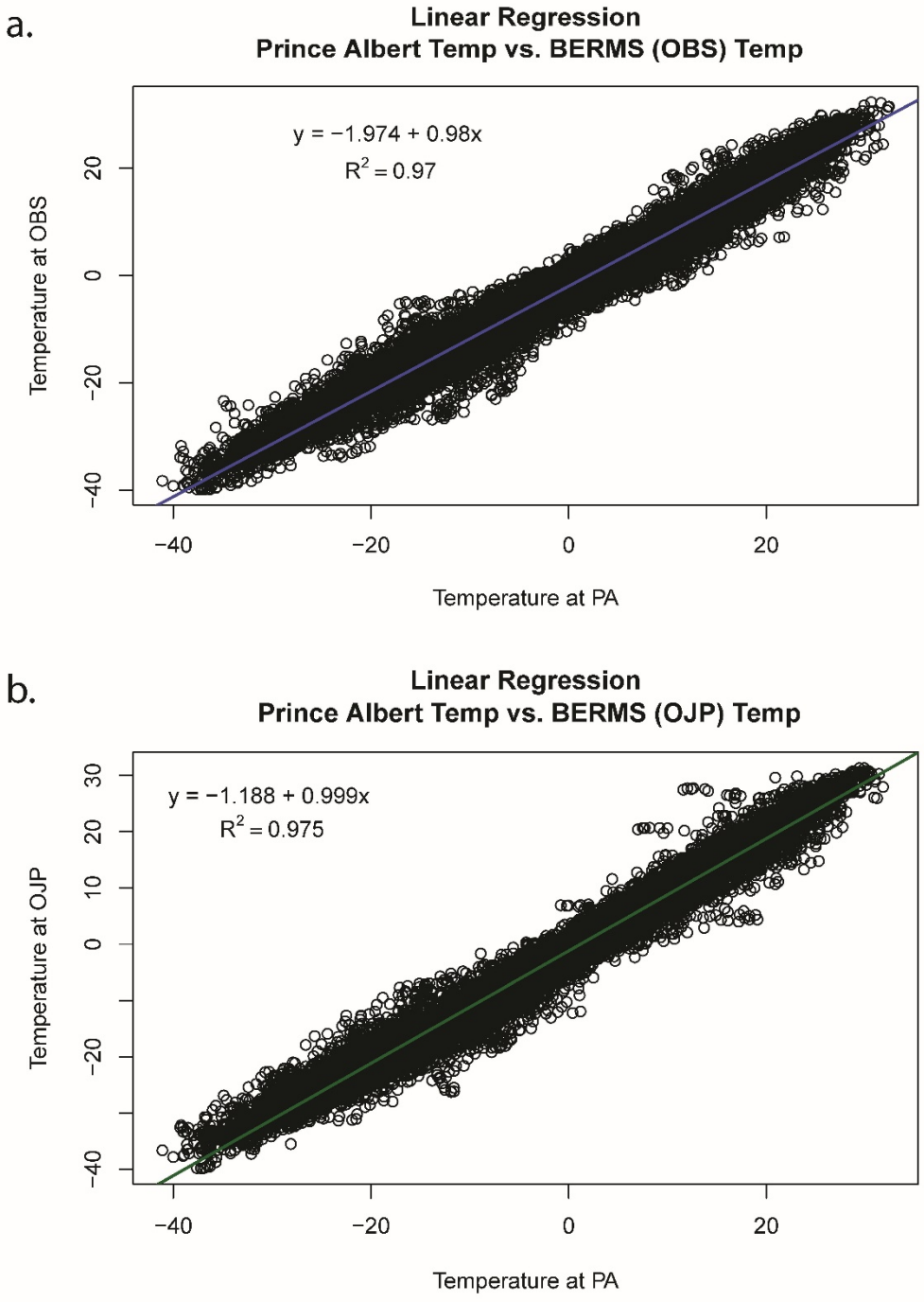
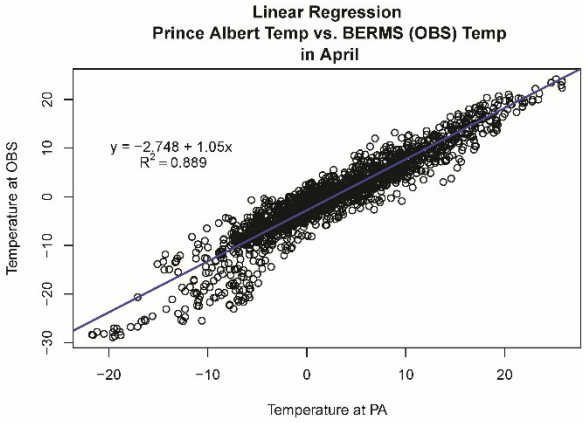
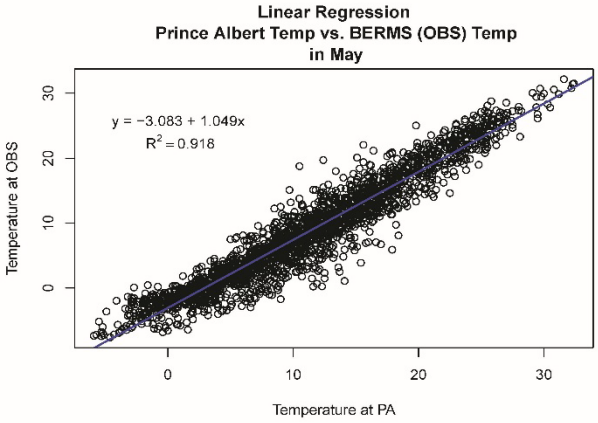
Appendix A

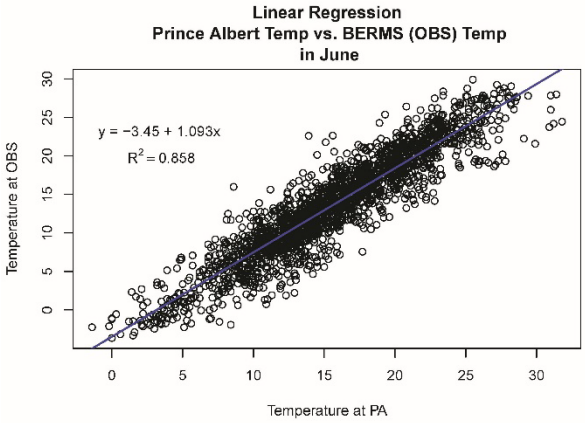


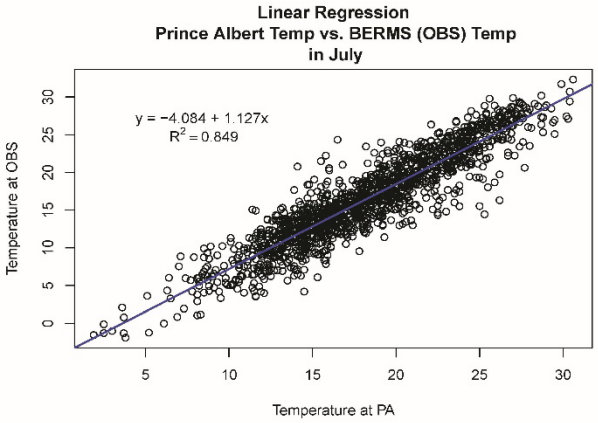
Linear regression between Prince Albert temperature and BERMS temperature. a. Linear regressions between Old Black Spruce site (OBS) and Prince Albert (PA); b. Linear regressions between Old Jack Pine site (OJP) used for FEN site and Prince Albert (PA).

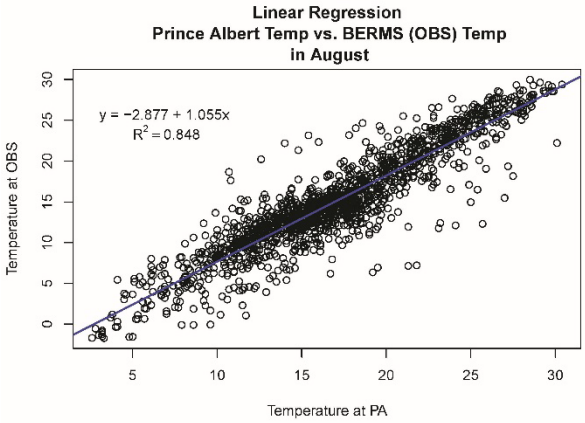
Monthly linear regressions (OBS)

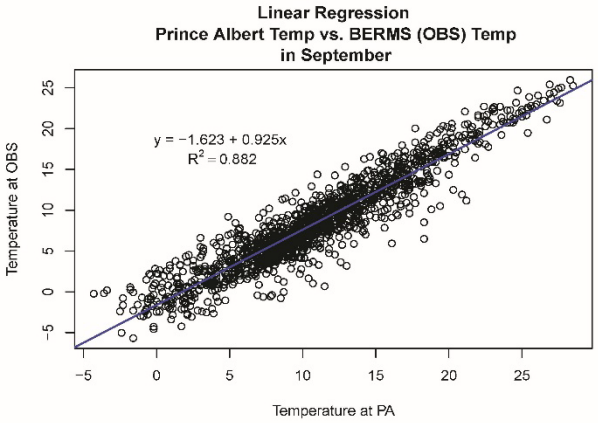


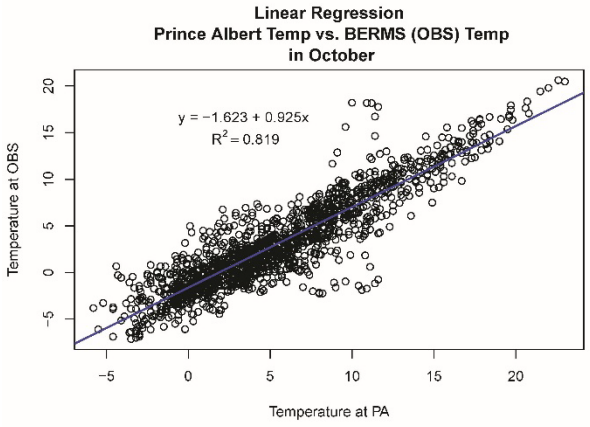


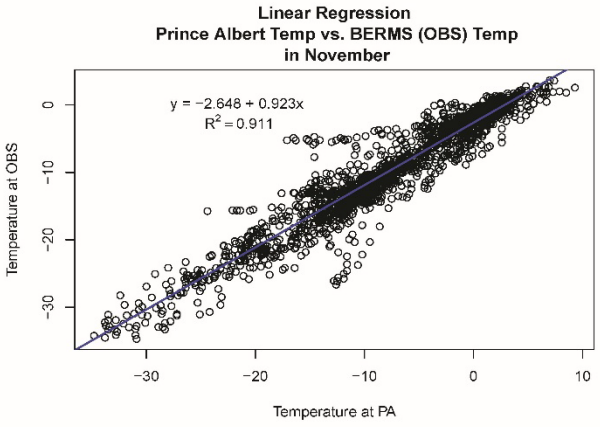


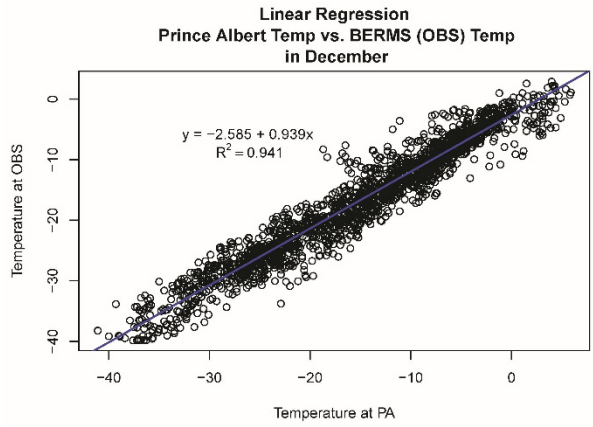


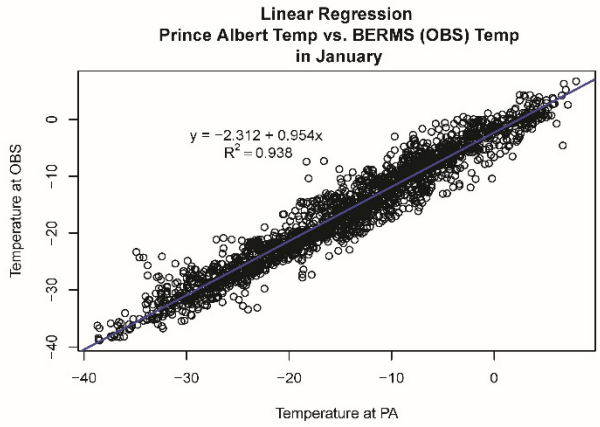


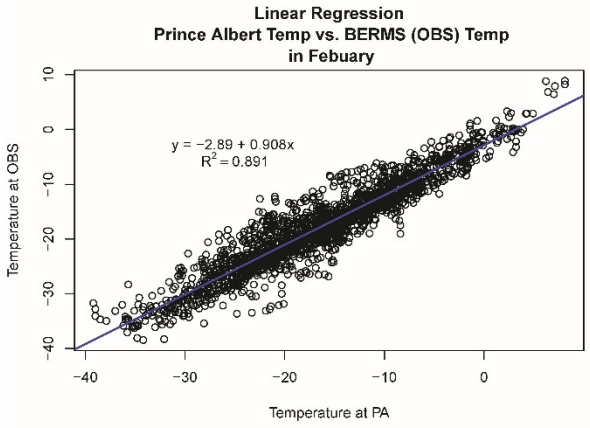


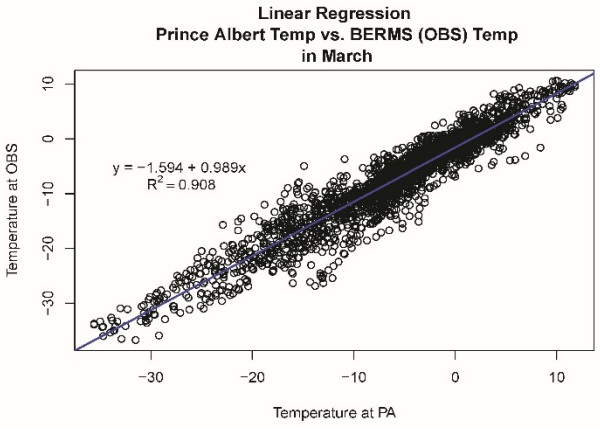

Linear Regression
Prince Albert Temp vs. BERMS (OBS) Temp
in October
y = −1.623 + 0.925x
R² = 0.819
Temperature at OBS
Temperature at PA


Linear Regression
Prince Albert Temp vs. BERMS (OBS) Temp
in November
y = −2.648 + 0.923x
R² = 0.911
Temperature at OBS
Temperature at PA

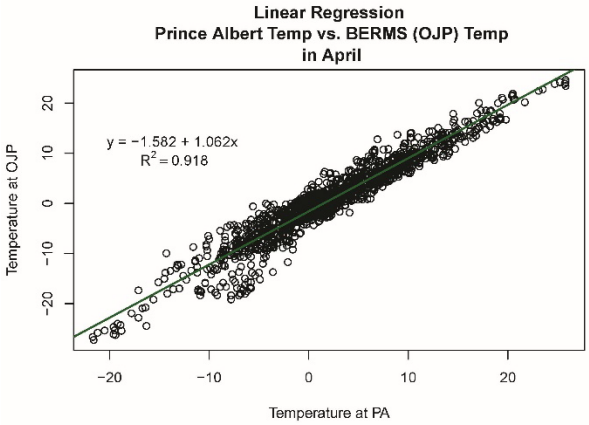

Linear Regression
Prince Albert Temp vs. BERMS (OBS) Temp
in December
y = −2.585 + 0.939x
R² = 0.941
Temperature at OBS
Temperature at PA

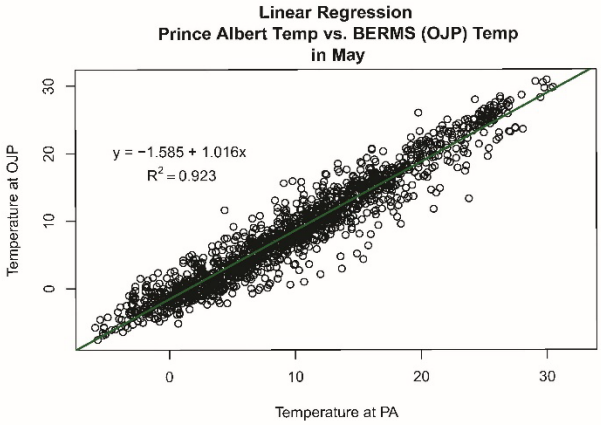

Linear Regression
Prince Albert Temp vs. BERMS (OBS) Temp
in January
y = −2.312 + 0.954x
R² = 0.938
Temperature at OBS
Temperature at PA

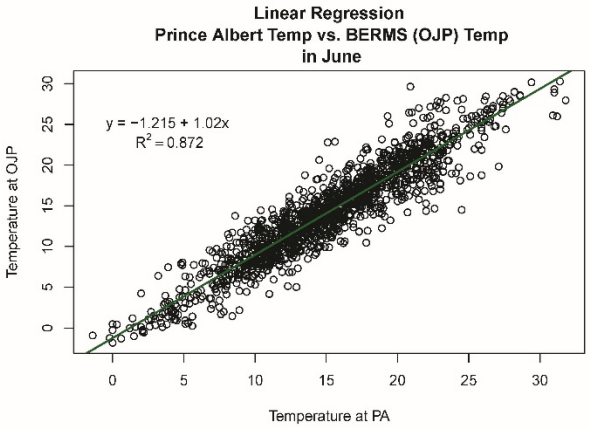

Linear Regression
Prince Albert Temp vs. BERMS (OBS) Temp
in Febuary
y = −2.89 + 0.908x
R² = 0.891
Temperature at OBS
Temperature at PA

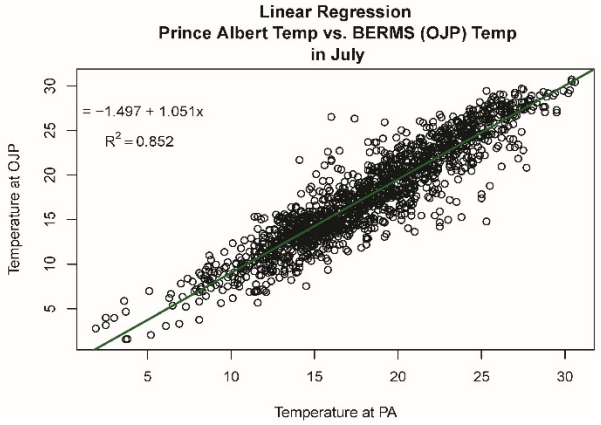

Linear Regression
Prince Albert Temp vs. BERMS (OBS) Temp
in March
y = −1.594 + 0.989x
R² = 0.908
Temperature at OBS
Temperature at PA

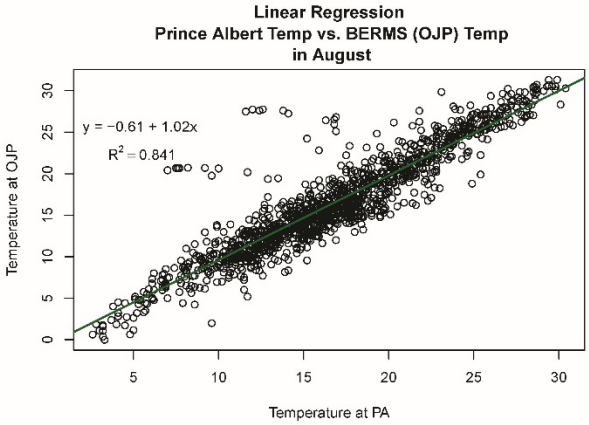
Monthly linear regression (OJP)

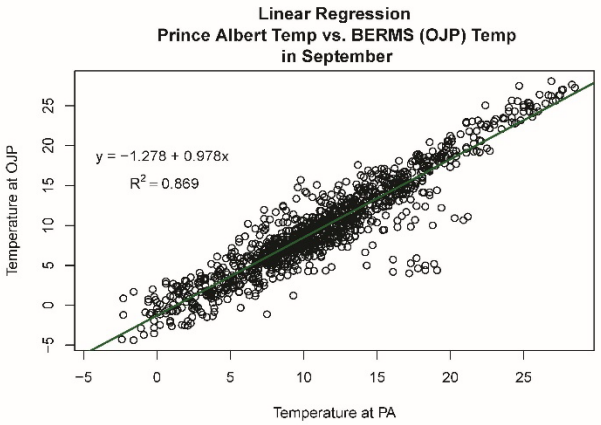


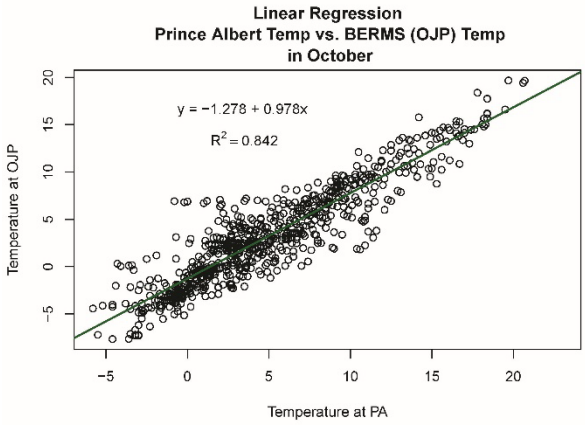


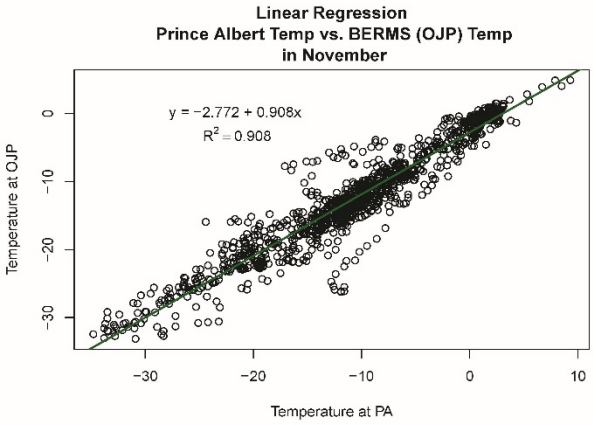


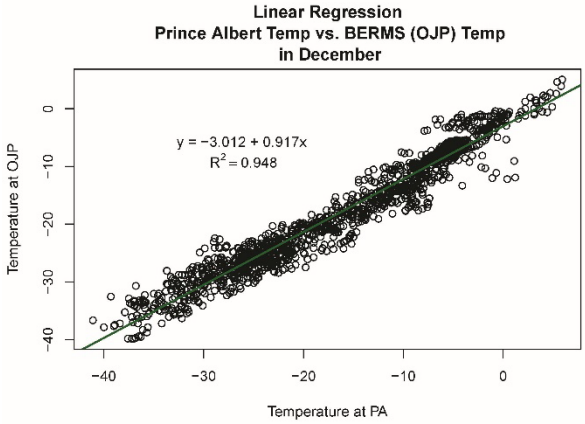


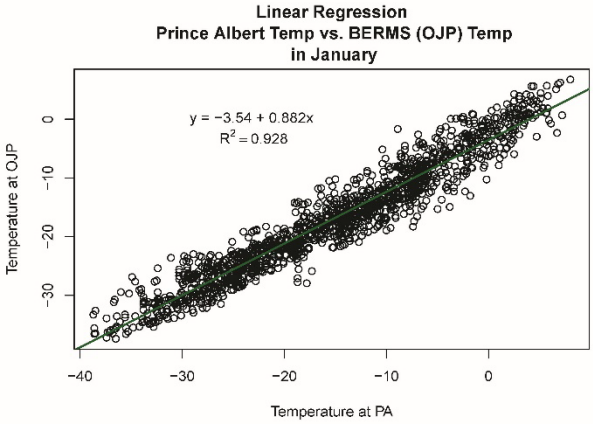


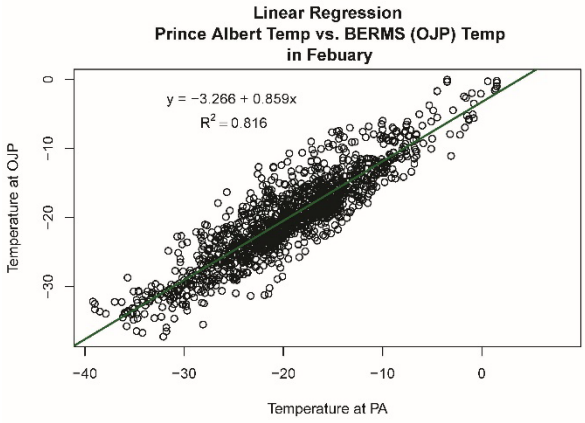


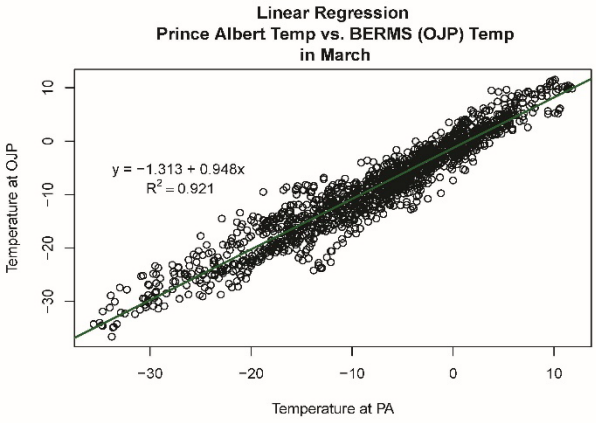

Linear Regression
Prince Albert Temp vs. BERMS (OJP) Temp
in October
y = −1.278 + 0.978x
R² = 0.842
Temperature at OJP
Temperature at PA


Linear Regression
Prince Albert Temp vs. BERMS (OJP) Temp
in November
y = −2.772 + 0.908x
R² = 0.908
Temperature at OJP
Temperature at PA


Linear Regression
Prince Albert Temp vs. BERMS (OJP) Temp
in December
y = −3.012 + 0.917x
R² = 0.948
Temperature at OJP
Temperature at PA


Linear Regression
Prince Albert Temp vs. BERMS (OJP) Temp
in January
y = −3.54 + 0.882x
R² = 0.928
Temperature at OJP
Temperature at PA


Linear Regression
Prince Albert Temp vs. BERMS (OJP) Temp
in Febuary
y = −3.266 + 0.859x
R² = 0.816
Temperature at OJP
Temperature at PA


Linear Regression
Prince Albert Temp vs. BERMS (OJP) Temp
in March
y = −1.313 + 0.948x
R² = 0.921
Temperature at OJP
Temperature at PA

Appendix B

Chronologies EPS values

LAO					
Start Year	***Mid Year***	***End Year***	***N° of cores***	***EPS***	***Coments***
1897	1901	1906	10	**-0.648**	
1902	1906	1911	21	**-1.415**	
1907	1911	1916	25	**-0.321**	
1912	1916	1921	27	**0.326**	
1917	1921	1926	33	**0.523**	Outbreak period
1922	1926	1931	34	**0.771**	Outbreak period
1927	1931	1936	36	0.886	
1932	1936	1941	36	0.932	
1937	1941	1946	36	**0.75**	
1942	1946	1951	36	**0.677**	
1947	1951	1956	37	**0.832**	
1952	1956	1961	37	**0.744**	Outbreak period
1957	1961	1966	37	**0.632**	Outbreak period
1962	1966	1971	38	0.887	
1967	1971	1976	39	0.941	
1972	1976	1981	39	0.971	
1977	1981	1986	39	0.978	
1982	1986	1991	39	0.963	
1987	1991	1996	39	0.985	
1992	1996	2001	39	0.981	
1997	2001	2006	39	0.964	
2002	2006	2011	39	0.982	
2007	2011	2016	39	0.968	
BSO					
Start Year	***Mid Year***	***End Year***	***N° of cores***	***EPS***	***Coments***
1895	1899	1904	24	0.958	
1900	1904	1909	32	**0.775**	
1905	1909	1914	35	0.929	
1910	1914	1919	38	0.922	
1915	1919	1924	39	0.934	
1920	1924	1929	40	0.932	
1925	1929	1934	40	0.91	
1930	1934	1939	40	0.94	
1935	1939	1944	40	0.946	
1940	1944	1949	40	0.909	
1945	1949	1954	40	0.957	
1950	1954	1959	40	0.967	
1955	1959	1964	40	0.968	
1960	1964	1969	40	0.971	
1965	1969	1974	40	0.964	
1970	1974	1979	40	0.93	
1975	1979	1984	40	0.968	
1980	1984	1989	40	0.979	
1985	1989	1994	40	0.963	
1990	1994	1999	40	0.948	
1995	1999	2004	40	0.914	
2000	2004	2009	40	0.929	
2005	2009	2014	40	0.939	

LACF					
Start Year	***Mid Year***	***End Year***	***N° of cores***	***EPS***	***Coments***
1947	1951	1956	10	0.861	
1952	1956	1961	10	**0.794**	Major outbreak and low sample depth
1957	1961	1966	15	0.851	
1962	1966	1971	23	0.932	
1967	1971	1976	25	0.941	
1972	1976	1981	31	0.944	
1977	1981	1986	34	0.976	
1982	1986	1991	38	0.96	
1987	1991	1996	38	0.957	
1992	1996	2001	38	0.961	
1997	2001	2006	38	0.982	
2002	2006	2011	38	0.981	
2007	2011	2016	38	0.965	
LAEF					
Start Year	***Mid Year***	***End Year***	***N° of cores***	***EPS***	***Coments***
1832	1836	1841	5	**-1.303**	Low sample depth
1837	1841	1846	7	**0.813**	Low sample depth
1842	1846	1851	8	0.89	
1847	1851	1856	11	**0.668**	
1852	1856	1861	11	**0.444**	
1857	1861	1866	11	**0.829**	
1862	1866	1871	13	0.869	
1867	1871	1876	14	0.85	
1872	1876	1881	16	0.89	
1877	1881	1886	19	0.862	
1882	1886	1891	21	**0.733**	
1887	1891	1896	21	**0.805**	
1892	1896	1901	21	**0.758**	
1897	1901	1906	21	**0.835**	
1902	1906	1911	22	**0.83**	Outbreak period (45%)
1907	1911	1916	22	**0.78**	Outbreak period
1912	1916	1921	22	**0.829**	
1917	1921	1926	22	**0.809**	
1922	1926	1931	22	**0.665**	
1927	1931	1936	24	0.9	
1932	1936	1941	31	0.956	
1937	1941	1946	37	0.944	
1942	1946	1951	37	0.943	
1947	1951	1956	37	0.971	
1952	1956	1961	37	0.948	
1957	1961	1966	37	**0.476**	Major outbreak period
1962	1966	1971	37	0.871	
1967	1971	1976	37	**0.833**	Outbreak period
1972	1976	1981	38	**0.786**	Outbreak period
1977	1981	1986	39	0.936	
1982	1986	1991	39	0.965	
1987	1991	1996	39	0.961	
1992	1996	2001	39	0.954	
1997	2001	2006	39	0.887	
2002	2006	2011	39	0.875	
2007	2011	2016	39	0.857	

BSF					
Start Year	***Mid Year***	***End Year***	***N° of cores***	***EPS***	***Coments***
1907	1911	1916	15	**0.84**	
1912	1916	1921	19	0.917	
1917	1921	1926	25	0.911	
1922	1926	1931	31	0.867	
1927	1931	1936	38	0.936	
1932	1936	1941	41	0.92	
1937	1941	1946	43	0.971	
1942	1946	1951	44	0.957	
1947	1951	1956	44	0.954	
1952	1956	1961	44	0.959	
1957	1961	1966	44	0.972	
1962	1966	1971	44	0.982	
1967	1971	1976	44	0.959	
1972	1976	1981	44	0.964	
1977	1981	1986	44	0.95	
1982	1986	1991	44	0.926	
1987	1991	1996	44	0.922	
1992	1996	2001	44	0.935	
1997	2001	2006	44	0.953	
2002	2006	2011	44	0.945	
2007	2011	2016	44	0.932	

Appendix C

Model performance evaluation

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(S_i - O_i)^2}{n}}$$

$$RSR = \frac{RMSE}{STDEV_{obs}} = \left[\frac{\sum_{i=1}^{n}(O_i - S_i)^2}{\sqrt{\sum_{i=1}^{n}(O_i - \bar{O})^2}}\right]$$

$$NSE = 1 - \frac{\left[\sum_{i=1}^{n}(O_i - \bar{O})^2 - \sum_{i=1}^{n}(S_i - O_i)^2\right]}{\left[\sum_{i=1}^{n}(O_i - \bar{O})^2\right]}$$

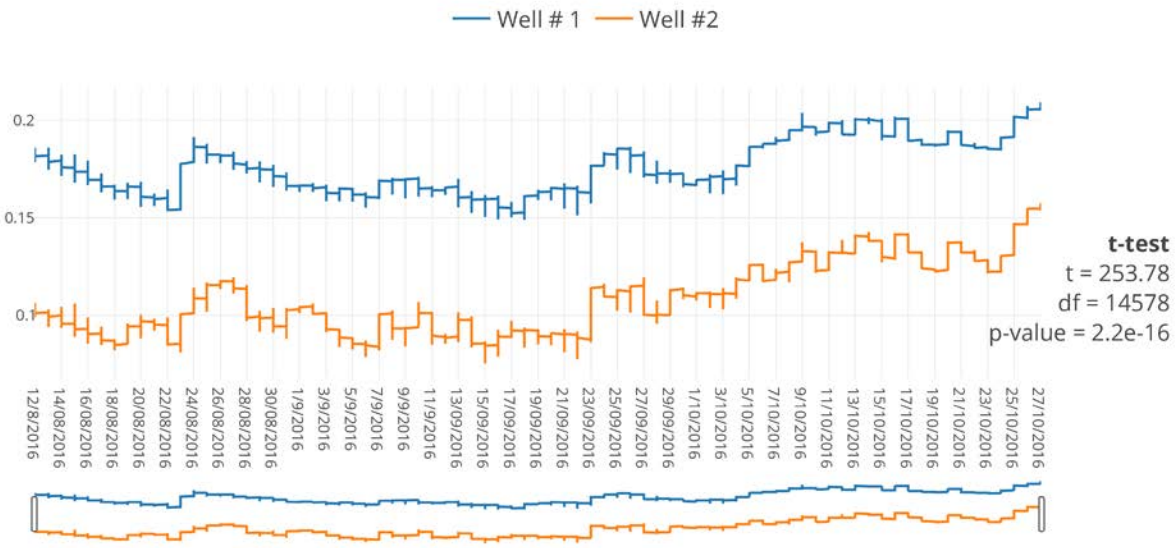
$$PBIAS = \frac{\left[\sum_{i=1}^{n}(O_i - S_i) * 100\right]}{\sum_{i=1}^{n}(O_i)}$$

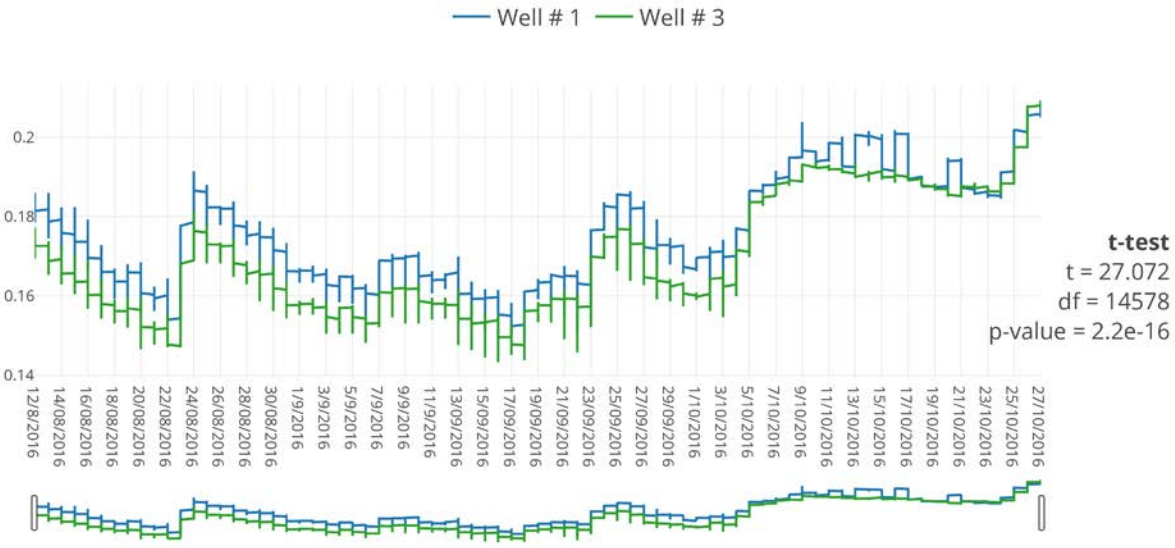
$$R^2 = \frac{\left[\sum_{i=1}^{n}(O_i - \bar{O})(S_i - \bar{S})\right]}{\left[\sqrt{\sum_{i=1}^{n}(O_i - \bar{O})^2}\sqrt{\sum_{i=1}^{n}(S_i - \bar{S})^2}\right]}$$

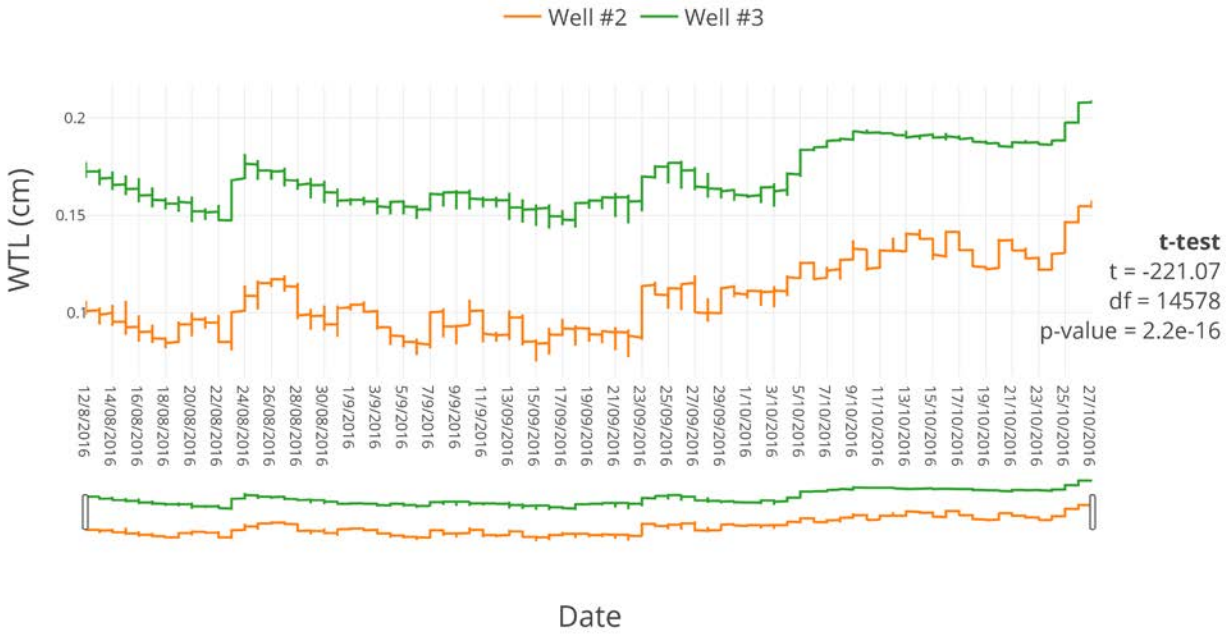
n is the number of observations in the period analyzed, O_i is the *i*-th observed value, Os the mean observed value, S_i is the *i*-th model-predicted value and *S*s the mean model-predicted value.

Appendix D

Water-table analysis

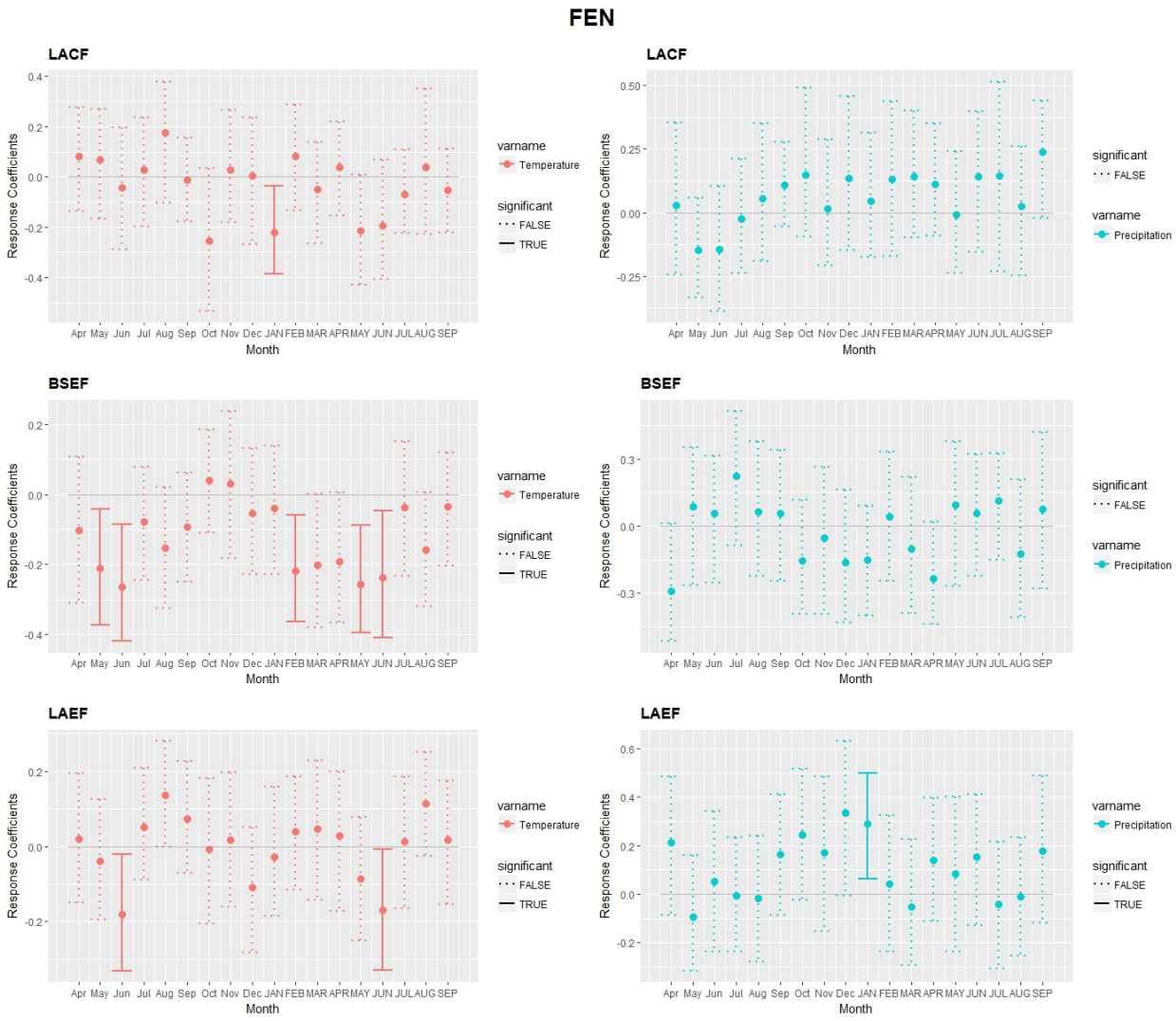




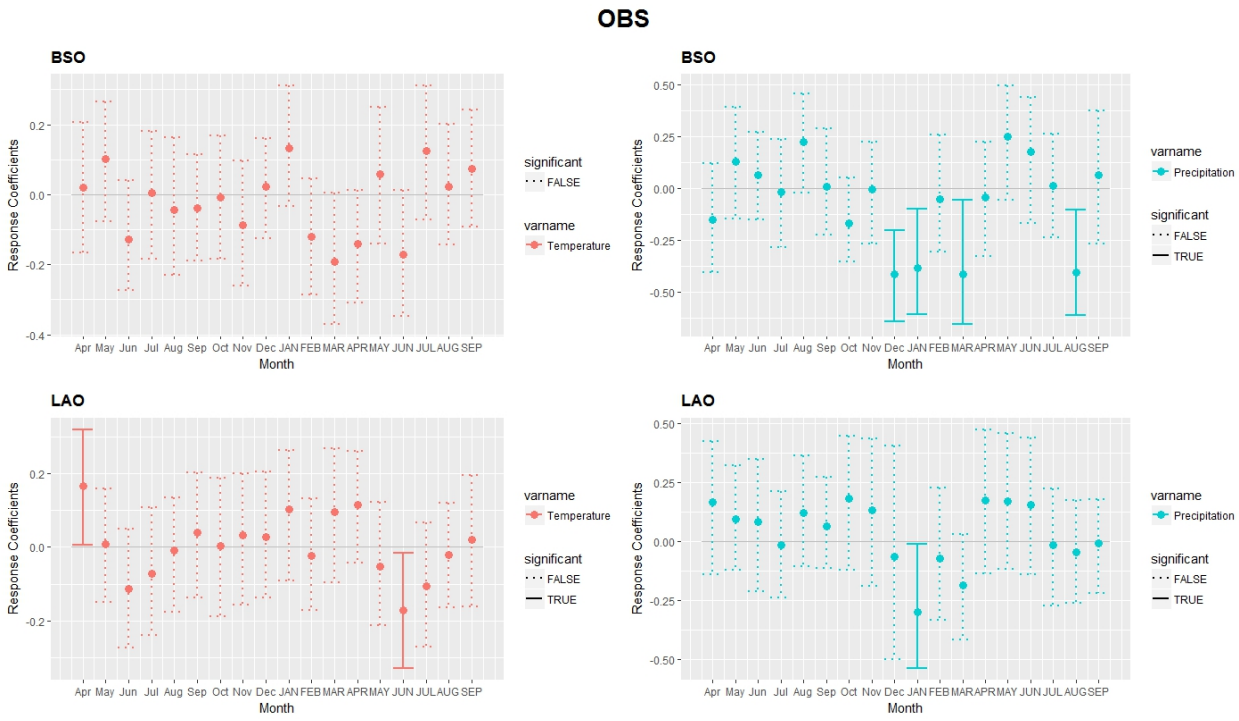

Well #2
Well #3
WTL (cm)
0.2
0.15
0.1
t-test
t = -221.07
df = 14578
p-value = 2.2e-16
12/8/2016
14/08/2016
16/08/2016
18/08/2016
20/08/2016
22/08/2016
24/08/2016
26/08/2016
28/08/2016
30/08/2016
1/9/2016
3/9/2016
5/9/2016
7/9/2016
9/9/2016
11/9/2016
13/09/2016
15/09/2016
17/09/2016
19/09/2016
21/09/2016
23/09/2016
25/09/2016
27/09/2016
29/09/2016
1/10/2016
3/10/2016
5/10/2016
7/10/2016
9/10/2016
11/10/2016
13/10/2016
15/10/2016
17/10/2016
19/10/2016
21/10/2016
23/10/2016
25/10/2016
27/10/2016
Date

Appendix E

Climate and tree-ring analysis

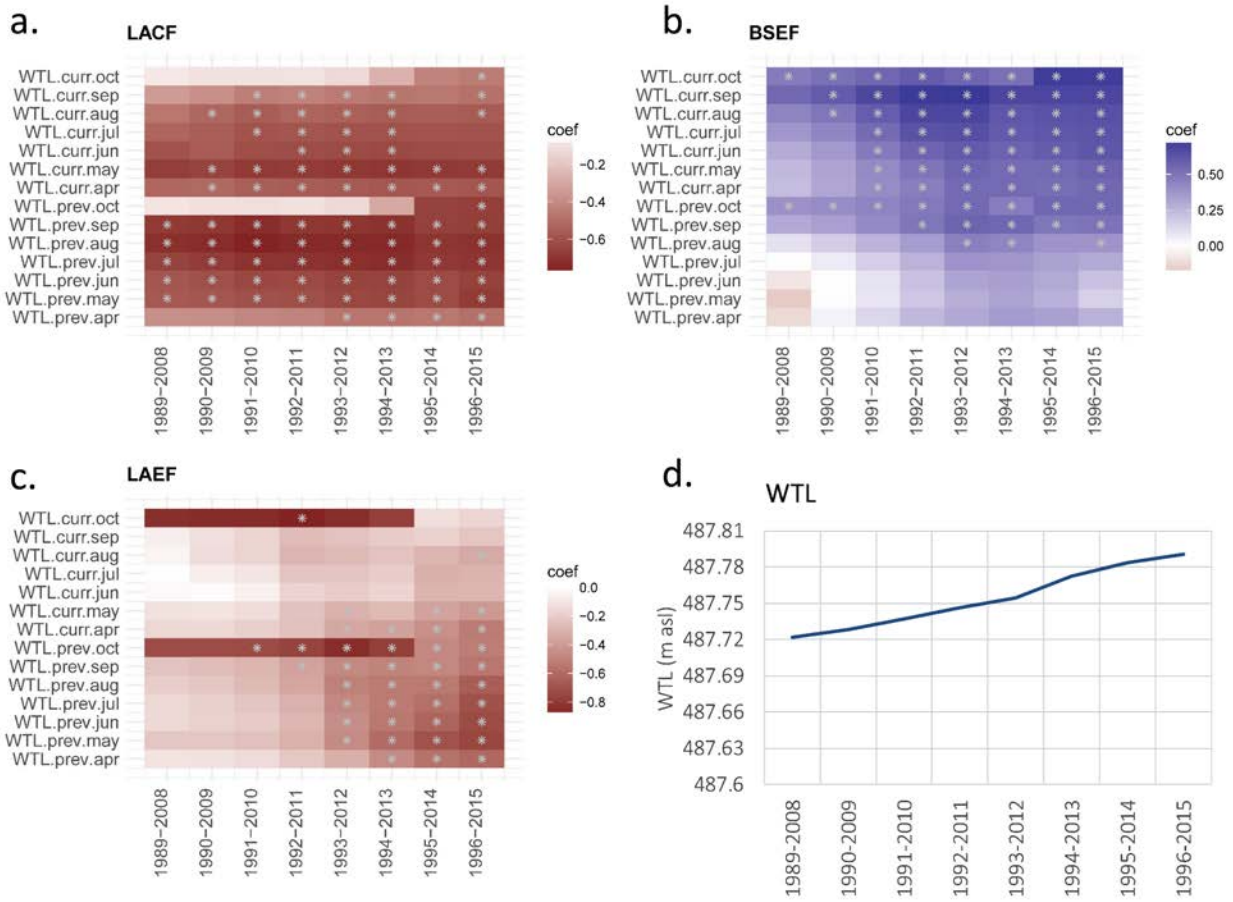


FEN - bootstrapped correlation analysis between temperature (red) and precipitation (turquois) and standard master chronologies from the FEN site: LACF (correlation interval: 1940-2015 - temperature; 1967-2015 - precipitation), BSEF (correlation interval: 1903-2015- temperature; 1967-2015 - precipitation) and LAEF (correlation interval: 1891 – 2015 - temperature; 1967-2015 - precipitation). The 18-month period was examined from April of the previous year to September of the current year. Lower case letters indicate months of the previous year, and upper case letters denote the current year' months. The full bars (TRUE) are significant above the 95%confidence interval.

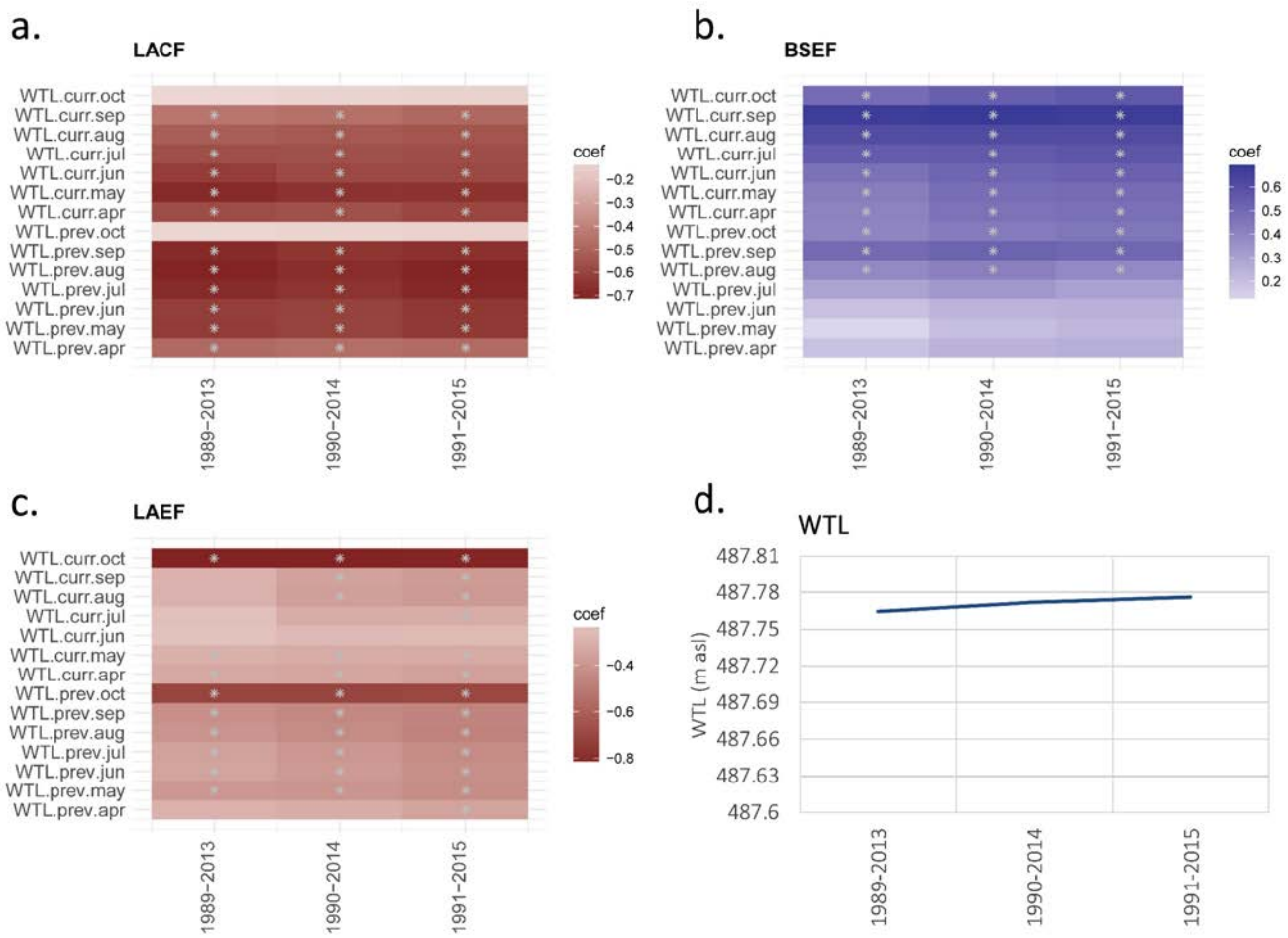


OBS - bootstrapped correlation analysis between temperature (red) and precipitation (turquois) and standard master chronologies from the OBS site: LAO (correlation interval: 1891-2015 - temperature; 1967-2015 - precipitation), BSO (correlation interval: 1891-2014- temperature; 1967-2014 - precipitation). The 18-month period was examined from April of the previous year to September of the current year. Lower case letters indicate months of the previous year, and upper case letters denote the current year' months. The full bars (TRUE) are significant above the 95%confidence interval.

Appendix F



Moving correlation analysis (20-year interval) (1989-2015) between standard master chronologies, a., b. and c., (LACF, LAEF, BSEF, respectively) and d. water-table level (20-year moving average interval) (WTL) in the FEN.



Moving correlation analysis (25-year interval) (1989-2015) between standard master chronologies, a., b. and c., (LACF, LAEF, BSEF, respectively) and d. water-table level (25-year moving average interval) (WTL) in the FEN.

Appendix G

Models	BSEF	LAEF	LACF-1 year	AIC	R2	adjusted R2	p-value
model 1	X	X	X	-52.53137	0.65	0.60	1.24E-05
model 2		X	X	-44.89204	0.50	0.46	1.65E-04
model 3	X		X	-54.36606	0.64	0.62	2.40E-06
model 4	X	X		-35.99358	0.32	0.26	8.74E-03
model 5	X			-37.78543	0.31	0.28	2.07E-03
model 6		X		-30.34265	0.10	0.07	1.00E-01
model 7			X	-43.83472	0.44	0.42	1.07E-04